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HEREDITY, VARIATION AND EVOLUTION IN PROTOZOA. II.

HEREDITY AND VARIATION OF SIZE AND FORM IN PARAMECIUM, WITH STUDIES OF GROWTH, ENVIRONMENTAL ACTION AND SELECTION.[1]

BY H. S. JENNINGS.

(*Read April 24, 1908.*)

TABLE OF CONTENTS.

(See pages 544–546.)

I. INTRODUCTORY.

The first of this series of studies[2] gave a general introduction to the investigations, and dealt with the fate of new or acquired characters in protozoa, showing that these are as a rule not inherited and that there is no difference in principle on this point between protozoa and metazoa. The present paper takes up heredity and variation in size and form in *Paramecium*.

Our present questions are then mainly as follows: In what respects do the individuals of *Paramecium* resemble each other? In what

[1] From the Laboratory of Experimental Zoölogy, Johns Hopkins University, Baltimore, Md.

[2] *Journal of Experimental Zoölogy*, Vol. 5, 1908, pp. 577–632.

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respects do they differ? What are the causes of the resemblances or differences, as the case may be?

The attempt is made to treat these questions broadly, determining experimentally the different classes of causes concerned, without prejudice as to their relative importance. External and internal factors are therefore equally considered, the purpose of the investigation being to give as complete an analysis of the phenomena of resemblances and differences as possible. Our problem, then, requires an analysis from this point of view of all things which may result in producing, increasing or decreasing the similarities and differences between individuals—reproduction, growth, conjugation, the effects of environment, of selection, and the like.

The investigation will be best introduced by proposing at once what is really the central problem—that concerning *heredity*. Is size inherited in *Paramecium?*

How would heredity of size be shown? If certain individuals differ in size, and the progeny of these individuals, under identical conditions, show corresponding differences, this is what would commonly be called heredity of size. "Heredity is a certain degree of correlation between the abmodality of parent and offspring" (Davenport, 1899, p. 35). Do large individuals of *Paramecium* produce, under the same conditions, larger progeny than do small ones? Is it possible to obtain by selection large and small races of *Paramecia?*

To study this question, we must first examine the variations in size commonly found in *Paramecium*.

II. PRELIMINARY STUDY OF VARIATION IN PARAMECIUM.

We owe our present knowledge of variation in *Paramecium* mainly to Pearl and his co-workers (see Pearl, 1907; Pearl and Dunbar, 1905). A more extensive work by Pearl on variation in *Paramecium* has been mentioned as in prospect; I learn from personal communication, however, that this is not to appear. I shall therefore publish my own results more fully than I should otherwise have done. Certain points in connection with variation in *Paramecium* have been dealt with by Simpson (1902) and Pearson

(1902); also by McClendon (1908). But we have at present nothing like a thorough analysis of the matter, based on extensive data.

1. General Methods of Work; Statistical Treatment and Its Uses.

Before we can study experimentally the nature and causes of the existing variations, we must, of course, know their extent, character and distribution. To this end I have made a statistical study, constructed frequency polygons, and determined the more important constants of variation and correlation. This has, of course, not been done because of belief in any occult virtue in mathematical treatment. Statistical methods have been used in this preliminary survey merely because they form the most natural and direct way of discovering and displaying the problems on which we wish to work; I doubt whether the most determined critic of the use of such treatment in biology could suggest any other way for our material. But I am fully convinced that "crucial evidence is always individual in the last analysis" (Whitman); that the preliminary statistical examination of the facts requires development as soon as possible into precise experimental knowledge. It is valuable to know just how many men out of a thousand will die in a given period, but it is infinitely more valuable to know which ones will die if the conditions are not changed, and why; and the latter knowledge includes the former. I have therefore advanced at once from the descriptive statistical work to experimental treatment. A curve or polygon of variation (such as Diagram 1) or a correlation table (such as Table I.) is to be looked upon as a mass of problems. The place occupied in the polygon or table by any individual is due to certain causes, and it is these causes that we seek.

In seeking these causes by experimental methods, statistical treatment is again found to be of the greatest value for detecting and registering the effects of single factors, under complex conditions. This method may be compared to a microscope; it enables us to detect and deal with causes and effects which we could not handle without it. I am convinced that it is a great mistake to hold that the only or the main use of statistical treatment is for "dealing

with the sphere of indefinitely numerous small causes—amenable only to the calculus of chance, and *not to any analysis of the individual instance.*" Such treatment is a most valuable instrument for precisely such analysis as will bring out the effects of individual factors when we are unable to experimentally disengage them completely from others; it aids us most essentially in the "analysis of the individual instance." Of this I hope the present paper may furnish illustrations. As Johannsen (1906, p. 98) has well expressed it, the mathematical treatment must, to give valuable results, be "based upon an accomplished sorting of the special facts and a biological setting out of the premises which are to be treated." Davenport (1899) states that "the statistical laws of heredity deal not with the relations between one descendant and its parent or parents, but only with the mean progeny of mean parents." The object of the present work is precisely to discover so far as possible the relation between one descendant and its parent (or other relatives); for this, statistical methods show themselves most useful.

2. A Typical Culture.

We will then first examine a typical culture of *Paramecium,* made in the usual way with pond water and decaying vegetation, in a circular glass vessel about nine inches across and three inches deep. This culture we will call *Culture 1.*

Inspection showed that *Paramecia* of markedly different size were found in this culture, so that it seemed a favorable one for a study of inheritance in size. Cursory examination seemed to indicate the existence of two sets of individuals, those of one set being nearly double the length of the others.

Of this culture a large number were killed on April 10, 1907, and four hundred specimens, taken at random, were measured as to length and breadth.

3. Methods of Measuring and Recording.

The animals were killed with Worcester's fluid, which is known to cause practically no distortion when properly used. Worcester's fluid consists of ten per cent. formalin saturated with corrosive sublimate. In using it, a large number of the infusoria must be brought into one or two drops of

water, then these must be overwhelmed with a considerable quantity of the fluid. If the infusoria are in a larger quantity of water, the killing takes place more slowly, the animals have time to contract, and distortion results.

The measurements were made on the slide, the organisms being either still in the killing fluid or in ten per cent. formalin. Transference to the latter has no effect on the form of the fixed animals. Most of the measurements were made directly with an ocular micrometer. In the case of cultures of large individuals, however, the form was projected on paper with the camera, in the way described by Pearl (1907), the extremities of length and breadth marked with the pencil, then these were measured with a scale made by projection of the ocular micrometer.

Such combinations of lenses were used that one division of the micrometer scale was equal to 4 microns (or in a few cases, which will be expressly noted, to $3\frac{1}{3}$ microns). The measurements were thus recorded in units, each of which was equal to 4 microns, so that the recorded units are multiplied by four to give results in microns. When the measurements fell between two lines of the micrometer, the line nearest the actual measure was that recorded; if the measurement fell just half way between two lines, the higher line was recorded. Thus, the recorded unit 45 included all measurements beginning with $44\frac{1}{2}$, and *less than* $45\frac{1}{2}$. In the tables, the measurements, given in microns, are therefore grouped about such values that each group includes values from two microns below to two microns above the one recorded. Thus, in Table 1, the length 180 includes all the specimens measuring from 178 up to (but not including) 182.

It will be well to summarize here, once for all, the method of treating the data obtained in the measurements. For most of the tables the constants computed (and recorded below the tables) were the following: the mean, standard deviation, and coefficient of variation, for length and for breadth; the mean index or ratio of breadth to length; and the coefficient of correlation. The computation of the constants was based on the well-known formulæ that have been brought together by Davenport (1904) and others. I used as a rule the actual methods set forth so clearly by Yule (1897). The computations were made by the aid of seven-place logarithms and of Crelle's and Barlow's tables. Two independent computations, at considerable intervals of time, were made in each case. While I cannot hope that errors in computation are excluded, I believe that such as may exist do not in any way affect the conclusions to be drawn.

Certain points of detail should be mentioned. While, as will appear, most of the tables do not give symmetrical curves, I have used only the simple statistical methods applicable in strictness to such curves; the methods are quite sufficient as a basis for the comparisons we wish to make.

In computing the standard deviation, Sheppard's correction of the second moment was used throughout. That is, if we employ the method of Yule (1897),

$$\sigma = \sqrt{\Sigma(f\xi^2) - d^2 - .08333},$$

or using the signs employed by Davenport (1904)

$$\sigma = \sqrt{\frac{\Sigma(V - V_0)^2}{n} - r_1^2 - \frac{1}{12}}.$$

TABLE I.

"Wild" Culture 1. Correlation Table for Length and Breadth of a Random Sample
(See Diagrams 1 and 2, polygons *A* and *a*.)

Length in Microns.

Breadth in Microns.	84	88	92	96	100	104	108	112	116	120	124	128	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	228	232	236	240	Totals.
28					1	4		5	3	5	2	3	4																												27
32	1	1			1	3	3	6	9	19	14	17	9	8	4	2																									97
36									3	2	6	5	9	7	7	3								1	1								1								45
40									1		1		3		5	2					2				1		2		1												18
44										1			2	1	2			1		1	1	2	1	2	4	1	3	7	9	5	3	6	4	1	1	1					59
48								1								1					2	1	3	3	1	4	2	7	5	5	4	8	11	5	1		1				65
52																						1			2	1	1	2	3	5	4	4	7	6	7	3	2	2			50
56																					1				1	1	2	1	1	3	1	5	1	2	2	4	1	3		1	30
60																						1										1		1		1	1	1	1		7
64																					1								1												2
Totals.	1	1	0	0	2	7	3	12	16	27	23	25	27	16	18	8	0	1	0	1	7	5	4	6	10	7	10	17	20	18	12	24	24	15	11	9	5	6	1	1	400

Mean Length, 165.840μ.
Mean Breadth, 48.860μ.
Mean Length of Left Hand Group, 125.420μ: of Right Hand Group, 200.972μ.
Mean Breadth of Left Hand Group, 33.396μ: of Right Hand Group, 49.216μ.

The *mean index* given below the tables is the mean of the quotient $\frac{\text{breadth}}{\text{length}}$: it shows essentially what percentage the breadth is of the length. This mean was found, without computing the index for each individual, by the following formula:

$$i = \frac{A_B}{A_L}(1 + C_L^2 - rC_BC_L).$$

Where i is the mean index, A_B is the mean breadth, A_L the mean length, C_B the coefficient of variation for breadth, C_L the same for length, and r is the coefficient of correlation between length and breadth.

I am greatly indebted to Dr. Raymond Pearl for assistance in the mathematical treatment of the data.

The results of the measurements of a random sample of 400 of Culture 1 are given in Table I.

It is evident on inspection of this table that the individuals fall into two well-marked groups, one set varying in length from 84 to 144 microns, the other set varying from 164 to 240 microns, while between these groups, in the region from 144 to 164 microns, only two specimens are found. The mean length for the entire sample falls at 165.840 microns, almost precisely in the region where no specimens are found. The smaller set have their mean length at 125.420 microns: the larger set at 200.972 microns.

These results are shown as frequency polygons in the lower portions of Diagrams 1 and 2.

4. Method of Constructing the Polygons.

In making the polygons for length, three units of measurement (12 microns) were grouped together to make a single unit of the abscissa of the polygon. This was done in order to destroy any irregularities due to unconscious prejudice on the part of the measurer for certain numbers. Thus, in measuring a large number of individuals, it may be found, for example, that few are recorded at 51, while at 50 there are many; or the reverse may occur. This is due only to the fact that in doubtful cases falling between these numbers the measurer unconsciously gives the preference regularly to one of them. The error thus introduced is extremely small (it can hardly be more than one micron in any case), but if the polygon is made without grouping together adjacent classes, there appear extreme irregularities in its outline, irregularities that are quite without significance. When three units are thrown together, any marked irregularities remaining in the polygons are almost certainly due to peculiarities in the material itself. It is of course possible that small peculiarities really existing may be hidden in

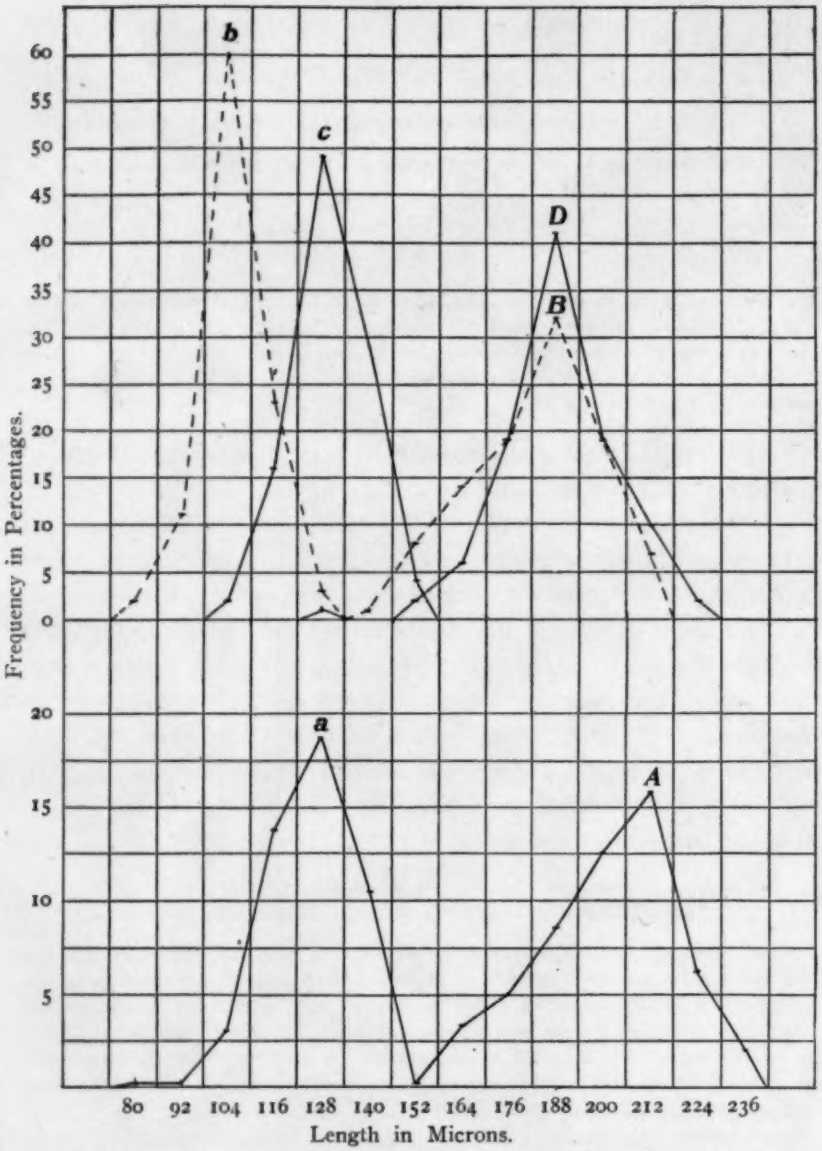

DIAGRAM 1. Polygons of variation for length in Culture 1 and its descendants. *A* and *a* form together the polygon for 400 specimens taken at random from the original culture 1, on April 10, 1907. *B*, polygon for 100 descendants of ten of the larger individuals of Culture 1. *D*, polygon for 100 descendants of the single large individual *D*, from culture 1. *b*, polygon for 100 descendants of fifty smaller individuals from culture 1. *c*, polygon for 100 descendants of the single small individual *c*, from culture 1.

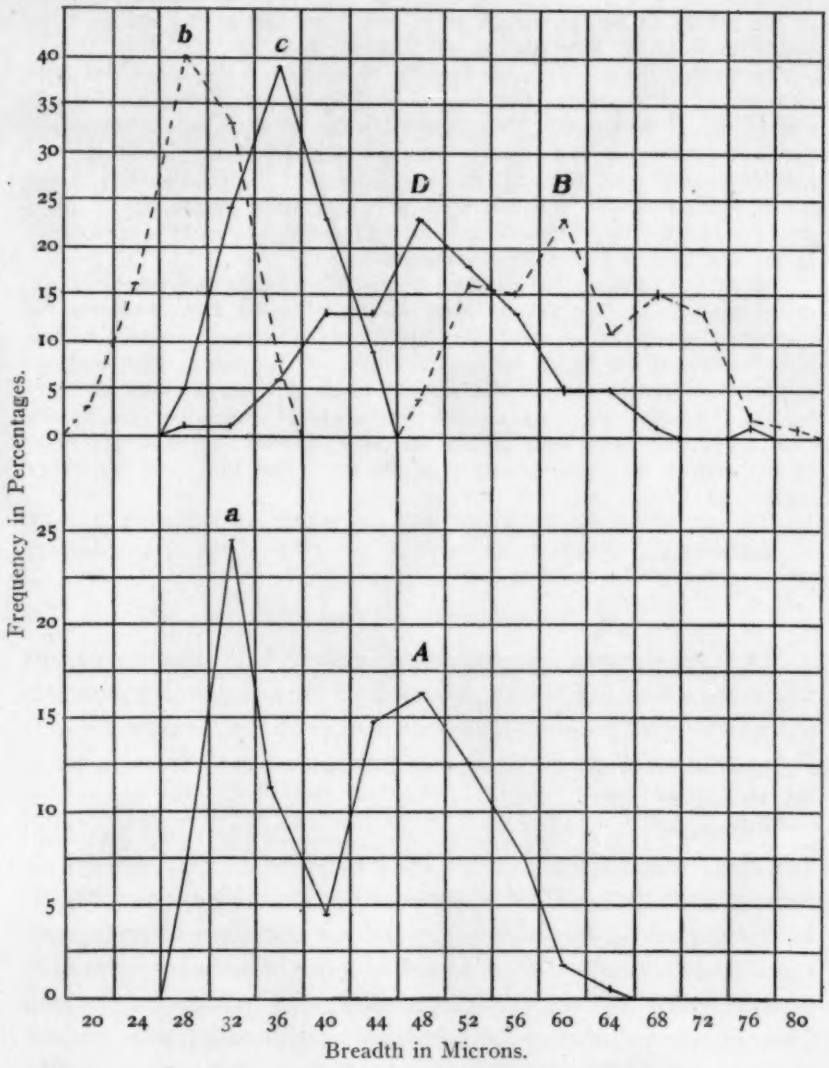

DIAGRAM 2. Polygons of variation for breadth in culture 1, and in its descendants from selected specimens. The letters have the same significance as in Diagram 1.

this way, but it was thought wiser to be conservative in this matter. Thus the space between two perpendicular lines of the polygons includes three of the groups of the correlation table, and is marked at its base with the middle value of the three groups which it includes.

In making the polygons for breadth, it was found that there was little evidence of error due to unconscious preference for certain numbers in making this measurement. This is probably due to the comparatively small numbers of units in the breadth measurement, and to the fact that it is possible to hold both limits of the measurement on the scale sharply in the eye at once, while this is hardly possible in measuring length. In the polygons for breadth, therefore, one unit of the polygon was made to correspond to one unit of measurement (four microns).

In all the polygons the numbers to the left indicate percentages of the entire number, so that all the polygons are of equal area, whatever the number of specimens on which they are based. The only exception to this is in the case of the double polygons *a* and *A*, of Diagram 1, resulting from plotting the random sample of Table I. Since this sample falls into two groups, the entire (double) polygon was made of twice the area of the other polygons. Each half polygon therefore becomes approximately equal to any one of the single polygons of the other diagrams, thus permitting ready comparison.

The numbers at the foot of the diagrams are the dimensions in microns. Each number corresponds to the value of the center of the column beneath which it stands.

5. Two Groups of Paramecia.

Thus the *Paramecia* in our natural culture I fall into two groups which are almost completely separated, so far as length is concerned, but which overlap a certain amount in breadth. Characteristic outlines of varied members of the two groups, drawn to the same scale, are shown in Fig. 1.

Are these two groups permanent differentiations, such as might be called distinct species, or are the differences possibly due merely to temporary dimorphism of some sort? To answer this question individuals of the two sizes were isolated and allowed to multiply separately, in cultures made of boiled hay. After varying periods of time 100 individuals, taken at random, were measured from each of these pure cultures, and the frequency polygon derived from these was compared with the two (nearly distinct) polygons from the original culture. The following cultures were made and measured:

1. Fifty of the smaller individuals were selected from the original culture, placed together, and allowed to multiply for twelve days (from April 10 to April 22). The measurements of 100 of this

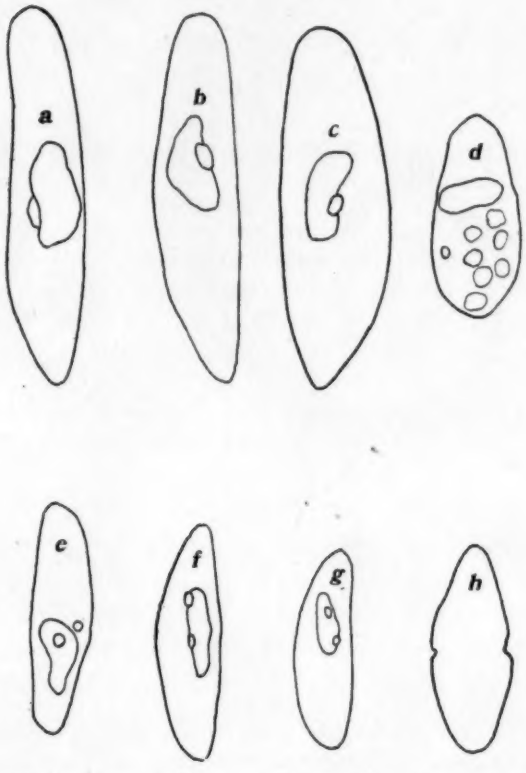

FIG. 1. Outline of characteristic specimens from the original wild culture 1, April 10, 1907. The upper row shows examples of the larger "*caudatum* form"; the lower row examples of the smaller "*aurelia* form." *d*, Young of the caudatum form; *h*, dividing specimen of the *aurelia* form. All × 235.

culture are shown in curve *b* (broken line), Diagrams 1 and 2; their dimensions are given in the correlation Table II. It is evident that this group corresponds in a general way with the smaller group of the original culture, though its mean length and breadth are somewhat lower (96.280 × 29.080 microns instead of 125.42 × 33.396), and it shows a little less variation.

2. Ten of the larger individuals selected from the original culture were likewise allowed to multiply in the same vessel for twelve days, then 100 were measured. The results are shown in curve *B*, Diagrams 1 and 2, and in the correlation Table III. It is evident

TABLE II.

Correlation Table for Length and Breadth of a Random Sample from Descendants of 50 of the Smaller Individuals from Culture 1, allowed to Multiply for 12 Days. (See polygons b, Diagrams 1 and 2.)

Breadth in Microns. \ Length in Microns.	80	84	88	92	96	100	104	108	112	116	120	124	128	
20					1		2							3
24					3	3	4	5		1				16
28					6	8	10	8	5	1	1		1	40
32	1	1	1			3	9	8	4	3	2	1		33
36									1	3	3		1	8
	1	1	1	0	10	14	25	21	10	8	6	1	2	100

Length—Mean, 96.280 ± .552μ Breadth—Mean, 29.080 ± .212μ
St. Dev., 8.160 ± .388μ St. Dev. 3.320 ± .168μ
Coef. Var., 7.678 ± .368 Coef. Var. 12.100 ± .585

Mean Index, or Ratio of Breadth to Length, 27.428 per cent.; Coef. of Cor., .3768 ± .0579.

that the progeny of these ten correspond to the larger set (*A*) of the original culture, though with slight differences in the means and in the amount of variation.

3. A single smaller individual, *c*, was selected from the original culture. As near as could be measured when alive, this individual

TABLE III.

Correlation Table for Length and Breadth of a Random Sample from Descendants of 10 of the Larger Individuals from Culture 1, allowed to multiply for 12 Days. (See polygons B, Diagrams 1 and 2.)

Breadth in Microns. \ Length in Microns.	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	
48		1		1	1			1											4
52			1	3	1	1	1	1	3		1	1	1	1				1	16
56	1		1	1	4		1	1			1	1	3		1				15
60					2	1	1	2		2	1	8	1	2	2	1			23
64								2	1	1	1	1	2	1	1		1		11
68							1			1	2		3	3	1	1	2	1	15
72									1	2	2	1	2	2		1		2	13
76														1	1				2
80										1									1
	1	1	2	5	8	2	4	7	5	7	8	12	12	10	6	3	3	4	100

Length—Mean, 182.760 ± 1.096μ Breadth—Mean, 61.360 ± .496μ
St. Dev., 16.264 ± .776μ St. Dev., 7.376 ± .332μ
Coef. Var., 8.899 ± .428 Coef. Var., 11.912 ± .576

Mean Index or Ratio of Breadth to Length, 33.652 per cent.; Coef. Cor., .5288 ± .0486.

was 120 microns in length. It was allowed to propagate in a culture free from all other *Paramecia,* from April 9 to June 11 (thus a little more than two months). Now a random sample gave the polygons shown at *c,* Diagrams 1 and 2; the measurements are given in Table IV. This group corresponds very closely to the smaller group *a* of

TABLE IV.

Correlation Table for Length and Breadth of a Random Sample Descended from the single small Individual c, taken from Culture 1 and allowed to Multiply 63 Days. (See Polygons *c,* Diagrams 1 and 2.)

Breadth in Microns. \ Length in Microns.	104	108	112	116	120	124	128	132	136	140	144	148	152	156	
28	1			2	1	1									5
32				2	6	5	5	3	3						24
36	1				3	8	8	7	5	1	4	1		1	39
40				1	1	2	5	3	3	4	3	1			23
44						1		1	2	2	2	1			9
	2	0	0	5	11	17	18	14	13	7	9	3	0	1	100

Length—Mean, 130.120 ± .628μ Breadth—Mean, 36.280 ± .260μ
St. Dev., 9.284 ± .443μ St. Dev., 3.880 ± .184μ
Coef. Var., 7.134 ± .342 Coef. Var., 10.700 ± .516

Mean Index or Ratio of Breadth to Length, 27.913 per cent.; Coef. Cor., .5208 ± .0492.

the original culture, though with slight differences in breadth.

4. A single very large specimen, *D,* approximately 250 microns in length, was isolated from the original culture on April 12 and allowed to propagate freely till June 11 (two months): 100 specimens taken at random then gave the measurements shown in the polygon *D,* Diagrams 1 and 2, and Table V.

Examination of the polygons and tables shows that the two forms retain their essential characteristics when isolated and propagated. The results shown in the diagrams are typical of many others. I have kept distinct strains of each of these groups for periods (at the present time) of more than eighteen months, and measurements made at frequent intervals during that time show that they have always remained quite distinct.

Thus it is clear that these colorless *Paramecia* fall into two distinct groups, which are at least relatively permanent. As is well known, two species of colorless *Paramecia* have long been distin-

TABLE V.

Correlation Table for Length and Breadth of a Random Sample Descended from the Single Large Individual D, taken from Culture 1, and allowed to Multiply 60 Days. (See polygons D, Diagrams 1 and 2.)

Breadth in Microns.	Length in Microns.																									
	128	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	228	
28	1																										1
32													1														1
36											1		2		1	2											6
40											2			3	4	3		1									13
44												1			3	4	2	1	1			1					13
48							1	1					4	1	3	5	1	2	1	1		2	1				23
52										1	1		3		2	2	3	2		2	1					1	18
56									1			1		2			2	2	1	1		2		1			13
60															1	2	1						1				5
64													1						1	1	1	1					5
68																				1							1
72																											0
76																		1									1
	1	0	0	0	0	0	1	1	1	1	4	2	11	6	14	18	9	9	4	6	2	6	2	1	0	1	100

Length—Mean, 188.360 ± .980μ Breadth—Mean, 49.000 ± .548μ
St. Dev., 14.532 ± .692μ St. Dev., 8.144 ± .388μ
Coef. Var., 7.715 ± .370 Coef. Var., 16.618 ± .814

Mean Index, 26.029 per cent.; Coef. Cor., .4188 ± .0556.

guished under the names *Paramecium aurelia* Müller and *Paramecium caudatum* Ehr. The two groups we have found correspond to the descriptions heretofore given of the two species, the smaller set representing *Paramecium aurelia,* the larger *Paramecium caudatum.* Besides the differences in size certain other characteristics have been held to distinguish the two species, and these distinguishing characteristics are evident in our two groups. *Paramecium aurelia* is described as having two micronuclei and *P. caudatum* but one; this is true for our larger and smaller groups respectively. *Paramecium aurelia* is said to be more rounded behind, while *P. caudatum* is pointed. In spite of many variations in form within each group, it is clear that our smaller group corresponds in this respect also with *P. aurelia,* the larger one with *P. caudatum.*

Calkins (1906) has brought forward evidence tending to show that the supposed distinction into permanently differentiated forms is not well based, so that there are not two species, the different sizes being merely variants of one. Calkins based his doubts as to the

really specific distinctness of *P. aurelia* and *P. caudatum* on the fact that in one of his pedigree cultures of *P. caudatum* the number of micronuclei changed from one to two, remained at two for many generations, and finally changed back again to one.

The results here published tend to indicate that the distinction into two groups is not without some sort of foundation. But it will be best to reserve the discussion of species until we have more data at hand. We may temporarily speak of the smaller set as the *aurelia* group, the larger one as the *caudatum* group. In a later part of the paper the question of distinguishing species will be taken up in detail, in the light of full data.

6. Are Differences in Size Hereditary within Each of the Two Groups?

We have found that among the variations of *Paramecium* in size are two groups, limited by internal causes, so that even under the same external conditions they differ in size; these two groups have heretofore been considered two species. But within each of these groups we find likewise many variations in size, so distributed, however, as to produce a curve with a single apex (Diagrams 1 and 2, etc.). These variations are at times very considerable, as will be evident from an examination of the polygons shown in Diagrams 3 and 6 (pages 413, 470), or the tables numbered VII. (page 412) and XX. (page 466). The next question to be considered is: Are the differences in size within such a group hereditary? That is, do the differences in size depend upon internal conditions, of such a character that the differences will persist in the progeny, even when the external conditions remain the same?

The experimental answer to this question is to be obtained by isolating individuals of different size belonging to one of the two groups (either "*aurelia*" or "*caudatum*"), allowing these to multiply and determining whether the progeny show differences in size corresponding to those in the parents. Can we by selection and propagation produce within the limits of a single group races of different mean size?

Experiments designed to answer this question were undertaken in the following way. As representing the *caudatum* group I

selected the cultures descended from the individual *D*; while the progeny of *c* represented the *aurelia* group. Now, from each of these groups the largest and smallest individuals were isolated and allowed to multiply, under uniform conditions. Thus, the selected large and small individuals of a given group were all *progeny of a single individual,* forming thus a "pure line"; this fact is of great importance, as the sequel will show.

A large number of experiments gave throughout negative results. The progeny of large and of small individuals (within a given pure line) *showed no characteristic differences in size.* Large specimens of the *caudatum* form produced progeny on the whole no larger than those produced by small specimens of the same form, and the same was true in the *aurelia* group. In many experiments a single large and a single small specimen were isolated, and their progeny compared; in other cases a number of large specimens were placed together in one vessel, a number of small ones in another, and their progeny compared after lapse of a considerable period. Since the results of these experiments were throughout negative, I will give the details of but a single illustrative experiment:

On July 27 ten large and ten small specimens were selected from a lot of the *caudatum* group, all being descendants of a single individual *D*. The ten large specimens measured, as nearly as could be determined while alive, approximately 250 microns each, and were thick in proportion to the length. The ten small specimens were about 150 microns long, and were thin. The two sets were placed in equal quantities of the same culture fluid.

At the end of three days the large set had produced many individuals. Fifty of these taken at random gave a mean length of 189.040 microns, a mean breadth of 60.560 microns.

The smaller individuals did not increase rapidly and five of them died before dividing, so that all the progeny came from six individuals. The six increased in size before dividing. At the end of three days there were twenty-one individuals. The mean length was 205.140 microns, the mean breadth 56.570 microns.

Thus the smaller specimens had produced progeny that were a little longer, but not quite so broad, as those resulting from the larger set. The existing differences are clearly without significance.

In other cases there was more variation in size among the different sets of progeny of *D*, particularly if the measurements were made after but few fissions had occurred. But sometimes the progeny of the large specimens were smaller, sometimes larger, than those of the small specimens. On the whole, both large and small specimens produced progeny of about the mean size for the group, under the given conditions.

Thus it is apparent that the differences in size shown within such a polygon as *D*, Diagram 1, are not due mainly to hereditary internal factors. Before we can determine with certainty whether any such factors are involved, we must make an analysis of the variation polygon, determining so far as possible the different factors, external and internal, which go to make it up.

7. Proposed Analysis of the Polygons of Variation.

Our present task is then to determine, so far as possible, what factors produce such polygons of variation as are shown in Diagram 1; to define what the individuals of different sizes and proportions really are, and to what their particular characteristics are due.

There are several sets of problems to be considered; these we may classify as follows:

1. What are the causes and the significance of the variations shown in a single variation polygon, such as *D*, Diagram 1? Why, in a group of *Paramecia* grown under the same conditions, and perhaps all descended from the same ancestor, do certain indviduals show the mean length, while others are larger and others smaller? Each size must have its determining factors.

2. In different polygons from *Paramecia* of the same general group and even when all are progeny of the same individual, the *mean* size differs much. Thus, in Diagram 6 (page 470) the mean length for polygon 8 is 146.108 microns; for polygon 11 it is 191.360 microns, though both represent descendants of the individual *D*, of the *caudatum* group. What are the causes of such variations in mean size among different sets of individuals?

3. In different sets of individuals belonging to the same general group, or descended from the same individual, the amount and range

of variation differs much. This is readily evident to the eye on comparing the polygon 8 of Diagram 6 and its correlation table, XIX. (page 466), with polygon 9 (Diagram 6) and its table, XX. In the former the length ranges only from 120 to 176 microns, and the coefficient of variation is 7.003, while in the latter the range of length is from 120 to 220, and the coefficient of variation is 12.767. What is the cause of these great differences in the variation of different groups?

4. In different sets belonging to the same general group the *correlation* between length and breadth differs greatly. Thus, in Table XX. (page 466) the correlation is high and positive, a difference in one dimension being accompanied, with much regularity, by a corresponding difference in the other. In Table XXXI. (appendix), on the other hand, there is almost no correlation, while in Tables XXIX. and XXXII. the correlation is marked, but negative —an increase in length being associated with a decrease in breadth, and vice versa. What are the causes and significance of these differences in correlation found in different sets?

In dealing with these questions, there are three main sets of possible factors to be examined, as follows:

1. *Hereditary Factors.*—Some of the factors concerned may be internal and largely independent of the environment—so that the differences in size are hereditary. The existence and nature of such factors form our main problem, but they can be dealt with only after the other factors are investigated.

2. *Growth.*—Some of the variations in size, and in proportions, may be due to different stages of growth, so that this matter must be carefully examined.

3. *Environmental Influences.*—It appears probable that the differences in the means, the differences in the range and amount of variation, and in the correlation, may depend partly on the nature of the environment.

We shall take up in detail these three sets of factors, beginning with growth.

III. GROWTH IN PARAMECIUM.

One significant fact was noted in the breeding experiments described in a previous section. Whenever a large and small specimen (belonging to a given group) were isolated at the same time, *the large specimen as a rule divided first.* Often at the end of forty-eight hours the large specimen had produced eight or sixteen progeny, while the small specimen had either not divided at all, or had produced but a single pair.

This suggests that the differences in size may be largely matters of growth; that the small specimens may be young ones, and that the variations shown in the frequency polygons may be largely growth differences. It is clear that a study of growth in *Paramecium* is imperative before intelligent work can be done with variation. The subject of growth in the Protozoa is an interesting one in itself, so that this study will be made as thorough as possible for its own sake, as well as for the light it throws on variation.

Growth was studied by three different methods: (1) By observation of abnormal specimens bearing localized appendages, noting the changes in position during growth; (2) by following the changes of form and size in living specimens; (3) by a statistical examination of the dimensions of individuals of known age.

The observations on growth in abnormal specimens have been described in my first communication (Jennings, 1908). By observations on the living specimen it is not possible to obtain precise measurements. It will be best therefore to begin our account with the statistical examination, taking up the observations on the living specimens by way of control.

Effects of Growth on a Variation Polygon.

If our suspicion that growth differences make up an important part of the observed variations in size of *Paramecium* is justified, then cultures rapidly multiplying and growing should be more variable than those that are stationary. To test whether this is true, two lots were removed from a rather old culture of descendants of *D,* in which inspection showed that the individuals were not multiplying rapidly. One of these lots was killed at once, while the other

was placed in fresh culture fluid. Twenty-four hours later this second set was found to be multiplying rapidly; a portion of it was then killed. The measurements of the two lots are given in Tables VI. and VII., while the facts are graphically represented in the

TABLE VI.

Correlation Table for Lengths and Breadths of a Random Sample from a Culture of Descendants of D, in which Multiplication was not in Progress. For comparison with Table VII. (See also Diagram 3.) (Row 3, Table XVIII.)

Length in Microns.

Breadth in Microns.	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	
32	1				2		1	1	3	1								9
36				2		6	5	1	2	2	2							20
40		1		1		3	8	4	4	4	3	1	3	3				35
44				1		1	2	2	2	3	3	4	1	3				22
48							1	1	3	2	1	3	4	3	1	4	2	25
52					1			1	1			2	1		2	3	4	15
56										1				2		1		4
60						1						1	1		2			5
	1	1	0	4	3	11	17	10	15	13	9	11	10	11	5	8	6	135

Length—Mean, 185.008 ± .836μ Breadth—Mean, 43.556 ± .392μ
St. Dev., 14.420 ± .592μ St. Dev., 6.748 ± .276μ
Coef. Var., 7.794 ± .324 Coef. Var., 15.490 ± .651

Mean Index, 23.517 per cent.; Coef. Cor., .5955 ± .0375.

TABLE VII.

Correlation Table for Lengths and Breadths of a Random Sample of Descendants of D, at a Time when Rapid Multiplication was in Progress. For comparison with Table VI. (See also Diagram 3.) (Row 4, Table XVIII.)

Length in Microns.

Breadth in Microns.	104	108	112	116	120	124	128	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	
32													2																		2
36										1	1	1	4	1	4	1	1	2		1											17
40								1		1	1	1	2	2	2		3	3	5	2	3	1	1	1							29
44	1					1	1	1	1	1	1	1	1	4	2			3	1	5	6	2	6	1	2						41
48			2	1						1	1	2				1	1	1		2	4	5	4	4	4	3	1				37
52			1	1				1				1						1	2	1	5	4	1	5	5	2					31
56	1																	1	2	3	1	3	2	3	2	4	1				23
60														1			1			1	2					2	3	1	1		12
64																	1		1												2
68																															0
72																					1										1
	2	0	3	2	0	1	1	3	1	4	4	6	9	8	8	2	7	11	11	15	22	15	14	14	13	11	5	1	1	1	19

Length—Mean, 176.124 ± 1.128μ Breadth—Mean, 47.364 ± .344μ
St. Dev., 23.360 ± .797μ St. Dev., 7.132 ± .244μ
Coef. Var., 13.262 ± .461, Coef. Var., 15.057 ± .526

Mean Index, 27.153 per cent.; Coef. Cor., .3945 ± .0408.

polygons of Diagram 3. It is evident that the variability has become much greater in the rapidly growing culture. The range of variation of length in the stationary culture is from 148 to 212 microns; in the growing culture it is from 104 to 220 microns, so that in the latter the range has almost doubled in extent. The coefficient of variation in length has likewise almost doubled, changing from 7.794 when the culture was stationary to 13.262 when it was growing. For breadth the range of variability has likewise increased considerably, though the coefficient of variability shows little change. The correlation between length and breadth has become considerably less in the rapidly multiplying culture, decreasing from .5955 to .3945. The mean length has slightly decreased, the mean breadth slightly increased, in the growing culture.

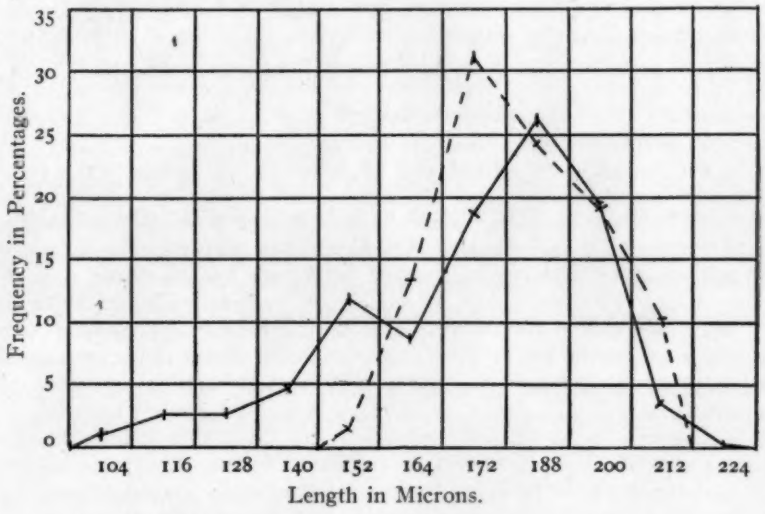

DIAGRAM 3. Polygons of variation in length for (*a*) a culture of descendants of *D* that is rapidly multiplying and (*b*) one that is not. The continuous line represents the rapidly multiplying culture of Table VII.; the broken line the stationary culture of Table VI.

From this example it is clear that growth and multiplication may, and probably do, play a large part in determining the character and distribution of the variations, as well as in determining the mean dimensions and their correlations. We shall now attempt to deter-

mine as accurately as possible what this part is by a systematic study of growth.

Material and Methods of Work.

In order to exclude possible differences due to different ancestry, the study of growth was made with the progeny of a single individual for each of the two groups. Of the *caudatum* group a single individual *D* was isolated April 12. This individual was a large one, measuring approximately 250 microns in length. From it many cultures were made under various conditions, and all the results on growth in this group were reached with progeny of this individual *D*, save in cases where the contrary is expressly stated. In the same way the results for the *aurelia* group were reached with the progeny of a single individual *c*, unless otherwise noted.

The method of work in the statistical study of growth was as follows: Numbers of dividing *Paramecia* of known descent were isolated and kept for varying periods, so that the age of the individuals was known to within a few minutes or even less. The individuals were then killed at different ages by the use of Worcester's fluid, and measured. In this way the usual size at various ages was determined, and those variations in size that are due only to varying age of the individuals were excluded. By pursuing this method, an approximate curve of growth is obtained and the part played by growth in the observed variations elucidated; much light is in this way cast on many obscure matters.

To persons who have worked with *Paramecium* it is unnecessary to point out the extremely laborious and time-consuming character of the operations required. Dividing specimens must be sought for with the microscope, among hundreds of their rapidly moving fellows; they must be taken up with the capillary tube, isolated, placed in culture fluid, and the time of capture noted. They must then, after lapse of the proper interval, be killed and measured; this is the smallest part of the work. To thus deal with individuals of known age by the hundred involves an incredible amount of exhausting labor, so that if the mathematical student finds in any stage the numbers employed not always as large as would be ideally desirable, he will realize that there is good reason for this. But it is hoped that the numbers used are amply sufficient, on the whole, for the purposes designed; the results are drawn from the measurement of over 1,500 specimens of known age; together with control cultures of mixed ages in still larger number.

Especially in the study of individuals that are very young (up to the age of half an hour or so), there is very great difficulty in dealing with large numbers owing to the fact that the time required for picking them out is very large in proportion to the amount of time they are to be kept, so that but few can be dealt with at once. Another great difficulty lies in the fact that to be strictly comparable, the sets of different ages must be chosen *on the same day from the same culture;* otherwise differences due to cultural conditions show themselves, confusing our results. No culture remains the same for two successive days, and the differences quickly show

themselves in the statistical results. The condition just mentioned cannot be absolutely fulfilled, but much effort was directed toward filling it as completely as possible, and where it could not be fulfilled, strict account of that fact was taken.

The fixing and measurement of the specimens was done by the methods already described (p. 396).

1. Description of Different Stages of Growth.

First Stage: the Young Before Separation is Complete.

In the earliest stage recognizable, the young *Paramecium* forms half of a dividing specimen. Before the constriction appears the macronucleus has become band-like, and the mother infusorian is shorter and thicker than the specimens not preparing to divide (see Fig. 2, *a*). The oral groove and other differentiated parts have become less marked. At the first appearance of the constriction the anterior and posterior halves still retain something of their characteristic form, and the body of the mother has extended a little (Fig. 2, *b*). The constriction does not pass squarely across the body, but is a little oblique, being farther back on the oral side (Fig. 2, *c*, *d*, *e*). As a result, when the two halves are measured separately, they will seem to differ in length, according to the place where the measurement is taken. Thus, if *d*, Fig. 2, is measured from the ends to the constriction along the oral side, the anterior half measures 96 microns, the posterior half 84 microns, while if the measurements are taken along the aboral side these proportions are exactly reversed. Measurements taken from one of the lateral sides give the same length for the two halves. The *Paramecia* may lie in various positions and this obliqueness of the constricting groove is not always evident. Misled by this fact, I took great pains to measure the precise length of each half in a large number of cases, finding considerable differences, though without any marked preponderance of either half. But I am now convinced that in early stages of fission the most accurate measurements of the young are to be obtained by considering each to be one half the length of the two together.

The breadth of the two halves frequently differs a little, the posterior half being at times slightly broader than the anterior half.

As the constriction deepens, the two halves lengthen (Fig. 2, *b* to *f*; *g* to *l*, etc.). This lengthening progresses with the advancing

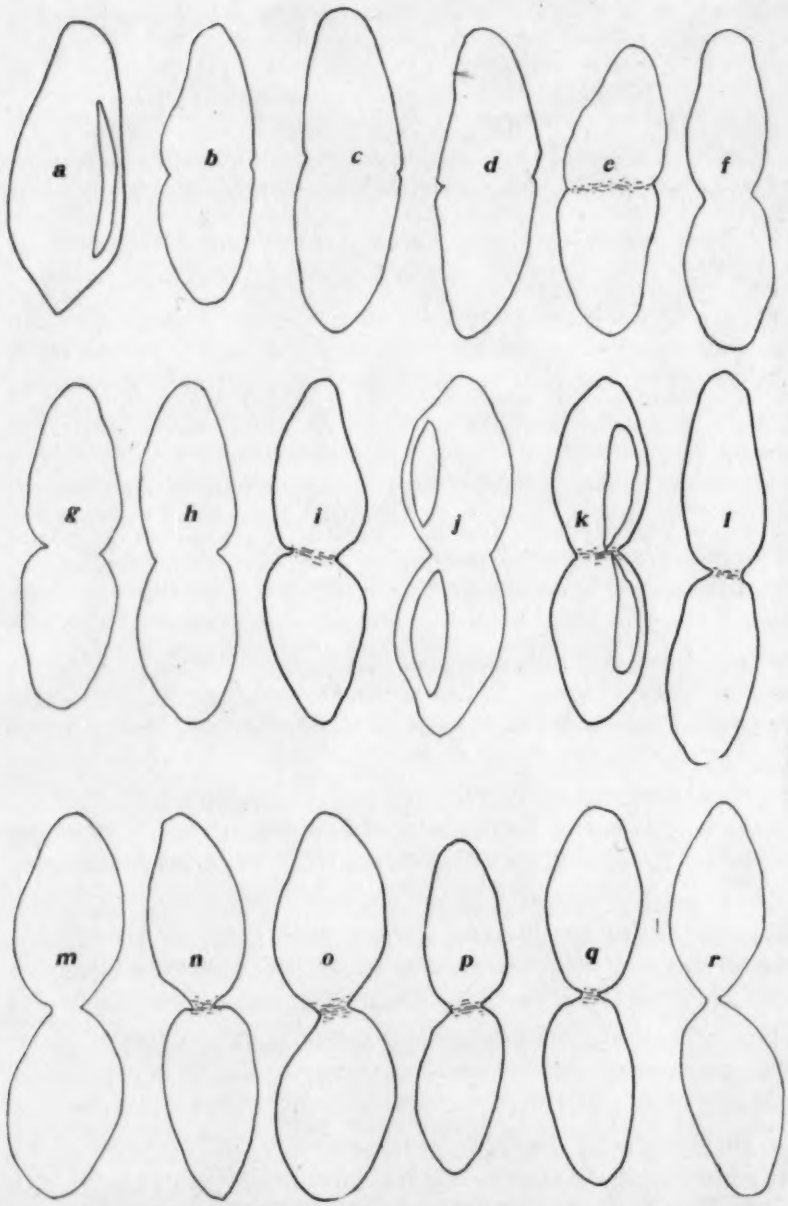

FIG. 2. Dividing specimens of the *caudatum* form, descended from the individual *D*. Note the increase in length and decrease in breadth as the constriction deepens. Anterior ends above. All × 235.

constriction until the two halves separate. This lengthening is clearly evident in the figures and in the correlation table giving depth of constriction with length of body (Table XI., page 441). As Table XI. shows, there is a period at the beginning, before the constriction reaches a depth of about 10 microns, when there is little relation between the length of the body and depth of constriction, showing that in this period the halves have not yet begun to lengthen. We may therefore take the length of the young at this period as that characteristic for the young individuals in their earliest recognizable condition, before growth has begun. By dealing with these alone we are able to compare the variability of the young with that of the adults, or with random samples including all ages. In the further treatment, therefore, the measurements of the unseparated young are divided into two classes: (*a*) those before lengthening has begun; (*b*) those after lengthening has begun.

(*a*) *The Unseparated Halves before Lengthening Has Begun.*—Studies were made of the young of three lots of the *caudatum* group (descendants of the individual *D*), and of two lots of the *aurelia* group (descendants of the individual *c*). Each "lot" included individuals taken on the same day from the same small culture. In most of the lots there were examined: (1) The unseparated young before growth had begun; (2) the unseparated young after growth had begun; (3) a random sample, including all sorts of individuals found in the culture. The results of these measurements are given in Table VIII., page 418.

(1) The *caudatum* Form (Descendants of *D*).—The most thorough study was made of lot 1, of the *caudatum* group; the results there reached are typical, and perhaps more reliable than any others, owing to the large numbers examined. We shall therefore make the results on this lot the basis of our discussion, afterward bringing out points of difference and resemblance shown in the other lots.

From this lot 1, I measured 313 dividing specimens, which, of course, included 626 unseparated young; a random sample of 200 individuals not dividing was likewise measured. A correlation table for the 313 dividing specimens, giving *the depth of the constriction* below the general body surface and the length is given on page 441

TABLE VIII.

Mean Dimensions and Constants of Variation for Youngest Stages, in Com-

is for convenience of reference in the text. The column headed which fuller data are given on the lot in question. A "Lot" consists of Table X., page 428.

Row.	A. *Progeny of D (Caudatum form).*	Number of individuals.	Table.	Length.		
				Mean.	Standard Deviation.	Coefficient of Variation.
1	Lot 1. Young halves, where depth of constriction is 4μ or less.....	262	9	87.848±.278	4.716±.197	5.368±.224
2	Lot 1. Halves, where depth of constriction is more than 4μ.....	364	(62)	93.033±.355	7.104±.251	7.636±.271
3	Lot 1. Random sample.....	200	14	199.960±.740	15.528±.524	7.765±.263
4	Lot 2. Halves, where depth of constriction is less than ¼ breadth.....	80	(43)	82.600±.468	4.394±.332	5.320±.402
5	Lot 2. *All* halves of dividing specimens.....	124	(42)	85.774±.593	6.924±.420	8.072±.492
6	Random sample.....	200	30	184.100±.776	16.264±.548	8.834±.300
7	Lot 3. Halves, depth of constriction less than ¼ breadth.....	84	(44)	83.810±.498	4.782±.352	5.706±.421
8	Lot 3. Adults 24 hours old.	300	41	168.532±.419	10.768±.296	6.389±.175
	B. *Progeny of c (aurelia form).*					
9	Lot 4. Halves, where depth of constriction is less than ¼ breadth.....	132	(47)	51.868±.325	3.912±.190	7.541±.445
10	Lot 4. Halves, lengthening begun (constriction more than ¼ breadth).....	106	(63)	60.692±.527	5.684±.372	9.365±.613
11	Lot 4. Random sample.....	225	49	114.163±.784	17.443±.555	15.279±.497
12	Lot 5. Halves, where constriction is less than ¼ breadth.....	76	48	56.666±.425	3.889±.302	6.862±.533
13	Lot 5. Random sample.....	100	50	114.033±.820	12.140±.580	10.646±.513
14	Lots 4 and 5. All halves where constriction is less than ¼ breadth (combination of rows 9 and 12).....	208	—	53.622±.300	4.535±.212	8.459±.398

(Table XI.). In 131 of these specimens the constriction had sunk less than one unit of the micrometer (4 microns) below the surface, while in the other 182 the depth of the constriction was greater. We may take the 131 specimens in which constriction had barely begun

TABLE VIII.—*Continued.*

parison with Random Samples and Adults. (The column headed "Row" "Table" gives the number of a table found elsewhere in the paper, in specimens all taken from the same culture on the same day.) Compare

Breadth.			Ratio of Breadth to Length, or Mean Index Per Cent.	Coefficient of Correlation.
Mean.	Standard Deviation.	Coefficient of Variation.		
55.480±.297	5.040±.210	9.082±.382	63.136	.6546±.0337
49.540±.215	4.296±.152	8.671±.309	53.592	—.0938±.0496
50.220±.308	6.468±.218	12.877±.441	25.114	.6064±.0302
50.700±.364	3.532±.260	6.769±.513	61.530	.1048±.1055
50.388±.307	3.584±.217	7.112±.433	59.166	—.1136±.0840
46.020±.251	5.256±.177	11.421±.390	25.084	.4282±.0389
65.716±.706	6.784±.499	10.322±.768	78.563	.2215±.0999
40.320±.230	5.892±.162	14.615±.411	23.899	.5496±.0272
34.850±.287	3.453±.203	9.911±.587	67.246	.6502±.0479
34.590±.383	4.147±.273	11.989±.797	57.296	.3100±.0837
34.207±.241	5.363±.171	15.683±.511	30.177	.6757±.0244
45.263±.597	5.463±.423	12.071±.947	79.806	.6744±.0597
47.300±.437	6.490±.310	13.720±.667	41.455	.8152±.0226
38.653±.437	6.607±.310	17.089±.822	71.835	.7476±.0292

as types of the earliest stage of fission, and their 262 halves as young *Paramecia* in the earliest stage. The lengths and breadths of these 262 halves are given in Table IX. The constants derived from the measurements of these, as well as from the measurements of the 364

TABLE IX.

Correlation Table for Length and Breadth of 262 Unseparated Halves of Dividing Specimens, in which the Depth of Constriction was less than four microns. All descendants of the single individual *D*, and taken from the same culture on the same day.

Breadth in Microns. \ Length in Microns.	78	80	82	84	86	88	90	92	94	96	98	100	102	
44		2		2										4
48	2	6	12	6	8	2		2						38
52		2	4	16	12	4	12	2	2					54
56		6	4	8	20	14	30	4	4	2	2			94
60			4	2	2	10	16	2	2	4	2			44
64					2		4	6	2	4	4			22
68										2		2		4
72													2	2
	2	16	24	34	44	30	62	16	10	12	8	2	2	262

Length—Mean, $87.848 \pm .278\mu$ Breadth—Mean, $55.480 \pm .297\mu$

St. Dev., $4.716 \pm .197\mu$ St. Dev., $5.040 \pm .210\mu$

Coef. Var., $5.368 \pm .224$ Coef. Var., $9.082 \pm .382$

Mean Index, 63.136 per cent.; Coef. Cor., $.6546 \pm .0337$.

halves in which lengthening had begun, and of the random sample, are given in the first three rows of Table VIII.[8]

We will for the present limit the discussion to the relations shown by comparing the youngest stages (row 1) with the random sample (row 3) which consists mainly of adults. The following important facts are shown:

1. The mean length of the youngest stages of the new individuals is considerably *less* than one half of the mean length of the individuals that are not dividing. The mean length of the young is 87.848 microns, while that of the individuals not dividing is 199.960 microns, or 24.264 microns more than twice the mean length of the young individuals. This remarkable relation will be taken up later, in discussing the measurements of dividing specimens (page 443).

2. The mean breadth of the youngest stages is slightly greater than that of adults not dividing—55.480 microns, in place of 50.220 microns.

[8] In Tables VIII. and IX. the measurements were made and the constants were first computed, for the entire dividing specimens. The constants for the halves were of course readily obtained from these; they are the same, save that the mean and standard deviation for length are halved, and the mean index is doubled. The computation of the probable errors was based on the *number of dividing specimens*, not on the number of halves.

3. The mean index, or ratio of breadth to length, is considerably more than twice as great in the young as in the adults; in the former it is 63.136 per cent.; in the latter 25.114 per cent.

4. The variability in length is less in the earliest stages of the young than in the individuals that are not dividing. In the former the coefficient that measures the variability is but 5.368, while in the latter it is 7.765.

5. The variability in breadth is likewise much less in the youngest stages—the coefficient being 9.082 in place of 12.877.

6. The correlation between length and breadth is nearly the same in the youngest stage as in the random sample, being .6546 in the former, .6064 in the latter.

From the other lots smaller numbers were examined. These gave on the whole similar results, though with certain significant differences. The facts are as follows:

From lot 2 (descendants of *D*), 124 halves were obtained. On account of the small number, I threw together all in which the depth of the constriction was less than one fourth the breadth, and considered these the earliest stage (the depth of constriction and length are given for the entire dividing specimens in Table XLII., appendix). There were thus obtained eighty young individuals (dimensions for the entire dividing specimens in Table XLIII., appendix). It is evident that this lot includes individuals varying more in age and growth than in lot 1, since in lot 2 we have included those having a much greater depth of constriction. The results are shown, in comparison with a random sample of the same lot, in rows 4 and 6 of Table VIII. The facts are in the main parallel with those for lot 1. As compared with the random sample, the mean length of the young is less than one half, the mean breadth a little greater, the mean ratio of breadth to length more than double, the coefficients of variation for length and breadth much less. A striking difference between this set and the young of lot 1 is that in the present case the correlation between length and breadth has decreased to such an extent that the coefficient computed (.1048) is without significance, being less than its probable error (.1055). This is due, as we shall clearly see later, to the fact that we have included in the

young of row 4 individuals older (constriction deeper) than in those of row 1.

From a third lot of descendants of *D*, 154 halves were obtained; in 84 of these the constriction was less than one fourth the breadth. Unfortunately no random sample of this culture was preserved. But 300 individuals just twenty-four hours old were taken from it for other purposes, and the young halves may be compared with these (rows 7 and 8, Table VIII.).[4] It should be noted, however, that the adults of row 8 had been kept for twenty-four hours in a rather small quantity of water, where food was relatively scarce, so that they were smaller than would have been the case if they had lived throughout under the same conditions as the dividing specimens.

In general, the same relations are shown here as in the other lots. A striking peculiarity is the great breadth of the young halves (65.716 microns), as compared with that of the adults (40.320 microns), so that the ratio of breadth to length (the "mean index") is more than three times as great in the young as in the adults (78.563 per cent. in the former, 23.899 per cent. in the latter). Owing to the inclusion of older halves, in which lengthening has begun, the correlation between length and breadth is again low ($.2215 \pm .0999$).

(2) The *aurelia* Form (Descendants of *c*).—Two lots of dividing specimens of the *aurelia* form were examined, the first including 132 halves in which lengthening had hardly begun, the second 76. The constants for these, in comparison with random samples of those not dividing, are given in rows 9 to 14 of Table VIII. These show the same relations that we have already seen in the *caudatum* group, with one exception. In the smaller collection (lot 5), the mean breadth of the halves was a little *less*, instead of greater, than that of the random sample. In this culture the animals were extraordinarily broad, the mean ratio of breadth to length in the random sample being 41.455 per cent., in place of the usual ratio of about 30 per cent. This was due to the fact that these animals had been placed twenty-four hours before in a rich nutrient solution and had

[4] The dimensions of the entire dividing specimens of which row 7 are the halves are given in Table XLIV. of the Appendix; the dimensions of the 300 just twenty-four hours old are given in Table XLI.

become very plump. The point of interest is that the breadth of the young individuals in the earliest stages tends toward a constant dimension, becoming greater when the adults are thin, less when the adults are plump. Outlines of dividing specimens, and of those not dividing, from this culture, are shown in Fig. 3, *a* to *f*; the great difference in breadth is noticeable.

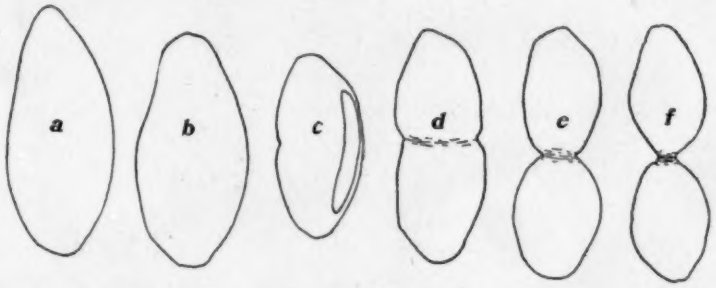

FIG. 3. Outlines of specimens of the *aurelia* form (descendants of *c*), from Lot 5, Table VIII. *c* to *f*, Successive stages of fission. Note the greater breadth of the specimens not dividing (*a* and *b*). Same magnification as Fig. 2. (235 diameters.)

In row 14, Table VIII., are given the constants for all the young halves examined of the *aurelia* group; that is, for the sum of rows 9 and 12. The coefficients of variation are, as might be expected, increased by adding these two dissimilar groups. The fact that the correlation between length and breadth is likewise increased, as compared with what we find in either group taken alone, might not, perhaps, be anticipated. These changes in variation and correlation are environmental effects, to be studied later.

(*b*) *The Unseparated Halves after Lengthening Has Begun.*— As we have already seen, the length of the halves increases as the constriction deepens (see the correlation tables for length with depth of constriction, Nos. XI. (page 441), XLV., XLVI.; compare also the outlines of dividing specimens, Figs. 2 and 3). The coefficient of correlation between depth of constriction and length is, for the 626 halves of Table XI., .6882; with each increase of 10 microns in depth of constriction the length increases 4.30 microns. If we include only the individuals in which lengthening has clearly begun (thus omitting the uppermost row of Table XI.), we find that for

these 364 halves the correlation between depth of constriction and length is greater, amounting to .7818; while the increase in length with each 10 microns of increase in depth of the constriction is 5.598 microns.

While the length thus increases, the breadth decreases. This is evident on inspection of Table XII. The correlation between depth of constriction and breadth of body is therefore negative; its coefficient, in the case of Table XII., is —.5232. With each increase of 10 microns in the depth of constriction the breadth of body decreases 2.630 microns. If again we take into consideration only the 364 halves in which lengthening has decidedly begun, omitting thus the uppermost row of Table XII., we find that the correlation decreases to —.3316, and the decrease in breadth for an increase of 10 microns in depth of constriction is but 1.252 microns. This appears to indicate that a large part of the decrease in breadth occurs in the first stages of constriction.

If we compare with the means of the 262 halves in which lengthening has not begun, the means of the 364 in which lengthening has begun (Table VIII., rows 1 and 2), we find that the length has increased from 87.848 to 93.033 microns, while the breadth has decreased from 55.480 to 49.540 microns. If we examine the means at successively older stages, we find, of course, greater differences. Thus, when the constriction has reached a depth of 36 microns, the 10 specimens in that stage show the mean length increased to 101.200 microns, while the mean breadth is but 46.400 microns. Similar relations are to be observed if we compare the means of the younger and older sets of each lot shown in Table VIII.

Since, while the length is increasing, the breadth is decreasing, the growth tends to decrease the correlation between length and breadth or even to make it negative. Thus, while in the stage before lengthening has begun (row 1, Table VIII.) the correlation is .6546, in the 364 specimens of the same lot, *after* lengthening has begun the correlation has decreased to —.0938 (row 2, Table VIII.). In a second lot, containing 124 halves, when we throw all the halves together the coefficient of correlation between length and breadth becomes —.1136 (row 5, Table VIII.). In the *aurelia* form, 106 halves after lengthening has begun give a positive correlation between

length and breadth of .3100 (row 10, Table VIII.). Why there should sometimes be a slight positive correlation, sometimes a negative one, at this stage, will be discussed in the section where we deal with the various factors determining correlation.

A variation polygon for the youngest stage of lot 1 of Table VIII. is shown in Diagram 4, p. 440, at *a*.

The changes above set forth from statistical data were in a number of cases observed in living individuals. These observations give a number of additional points of importance, so that they will be described. The facts, as illustrated mainly by a typical specimen of the *aurelia* form, are as follows:

Some time before fission the body thickens and becomes shorter, taking the form shown at *a*, Fig. 2, or *c*, Fig. 3. The form and dimensions differ very noticeably from those of the specimens not preparing to divide. How long before the appearance of the constriction these preparatory changes in form begin it is not possible to say, because it is not possible to distinguish with certainty whether a given specimen is to divide or not until we can see the constriction, and this is at a relatively advanced stage of the process. At the time the constriction first appears the anterior and posterior halves still differ in form, though they are losing their characteristic features.

As the constriction deepens the two halves become longer (Fig. 2, *b* to *f*, Fig. 3, *c* to *d*). A specimen of the *aurelia* form (descendant of *c*) was at about the stage shown at *d*, Fig. 3, at 12.05; each half measured very nearly 80 microns in length.

Ten minutes later (at 12.15) the connecting portion had become smaller, while the two halves had lengthened, so that each measured about 85 microns in length. The anterior half was more pointed and slightly more slender than the posterior half (*f*, Fig. 3); this is regularly the case.

Six minutes later (at 12.21) the posterior half measured about 90 microns, the anterior half 94. The connecting band was now extremely slender.

Five minutes later (at 12.26) the two halves separated. The anterior half was still clearly distinguishable from the posterior one by its pointed, somewhat pear-like form. It measured 100×44

microns, while the posterior half was shorter, but thicker, measuring 96 × 52 microns. The succeeding changes of form will be described in the next section.

Thus from the condition shown at *d*, Fig. 3, to the completion of fission a period of twenty-one minutes elapsed. From the earliest appearance of the constriction the time till separation is usually a little more than one half hour.

Second Stage: the Young Immediately after Fission up to the Age of Ninety Minutes.

Observation of Living Specimens.—Immediately after separation of the two halves, growth occurs rapidly, and the shape changes, both halves becoming more pointed at both ends. In the specimens of the *aurelia* form under description at the close of the last section, the posterior half had two minutes after fission increased in size from 96 × 52 microns to 104 × 48 microns. Eight minutes after separation both halves measured 112 microns in length, so that they had during that period increased respectively 12 and 16 microns in length. The difference between anterior and posterior individuals was still marked.

Now followed a period of slower growth. At 12.53, twenty-seven minutes after division, each half measured approximately 120 microns in length. They had taken nearly the characteristic adult form and it was no longer possible to distinguish the anterior product from the posterior one.

At 2 P. M. (one hour and thirty-four minutes after separation) the length was about 135 microns and the progeny were similar to the adult specimens of the *aurelia* form.

Thus, at the time of separation the two individuals have somewhat more than half the adult length; they grow rapidly at first, then slowly, and in an hour and a half have reached nearly the adult size. (As later statistical studies show, growth continues for a long time still.)

Observation on the growth of living specimens of the *caudatum* form gave a parallel series of phenomena (see Fig. 4). Thus, in a descendant of D_1 the length of each half at the time of separation

was about 120 microns; width 48 microns. Five minutes later the length had increased to 132 microns, while the width was still 48 microns. Nine minutes later the length of the anterior product was 148 microns; that of the posterior product 144 microns. The width had decreased a little; it was now about 44 microns.

After thus increasing in fourteen minutes by nearly one fourth the original length, growth became less rapid. Forty minutes later (fifty-four minutes after separation) the length was about 156 microns. During two succeeding hours no increase in length could be detected. The form was that of the normal adult, though the adult size was not yet reached.

We may summarize as follows: Some time before fission (perhaps a half hour) the body shortens and thickens, so that each half is at first less than half the adult length. As the constriction deepens the two halves grow longer, till at the time of separation they are somewhat more than half the adult length. For five to twenty minutes after separation growth in length is very rapid, while the thickness remains stationary or decreases. Then follows a period of several hours of slower growth, till the adult size is reached.

This somewhat indefinite account, based on the observation of living specimens, will now be supplemented by a statistical investigation of a large number of individuals at various ages. The main results of this statistical investigation are brought together in Table X.

(*c*) *Age 0 to 5 Minutes* (*Table XXIX.*).—A large number of dividing specimens, all descendants of the individual *D* (*caudatum* form), were removed from a rapidly multiplying culture and kept for from 0 to 5 minutes in a watch-glass of culture fluid, then killed and measured. The method of work was to spend five minutes in picking out dividing specimens with the capillary tube and placing them in the watch-glass; at the end of the five minutes the lot was killed. Then other lots were prepared in the same way. In each lot killed, therefore, there occurred specimens that were in the early stages of fission; others that had separated at the moment of removal and were hence just five minutes old; and all stages intermediate between these two. All together, 62 unseparated pairs and 59 separated individuals were secured in this way. The latter set consists of individuals from 0 to 5 minutes old (reckoning from the moment

TABLE X.

Dimensions and Constants of Variation for Paramecia of Various Ages, in taken from the same culture on the same day. The lots where identical column headed "Row" is for convenience of reference. The column elsewhere, in which fuller data are given on the lot in question.)

Row.	A. *Progeny of D (Caudatum Form).*	Number of Individuals.	Table.	Length.			
				Mean in Microns.	Standard Deviation in Microns.	Coefficient of Variation.	Range of Variation in Microns.
1	Lot 1. Youngest unseparated halves, constriction beginning	262	9	87.848± .278	4.716± .197	5.368± .224	78–102
2	Lot 1. Halves, lengthening begun	364	(62)	93.033± .355	7.104± .251	7.636± .271	80–112
3	Lot 1. Random sample.	200	14	199.960± .740	15.528± .524	7.765± .263	148–240
4	Lot 2. From beginning of constriction to 5 minutes after separation	183	—	92.940± .718	14.400± .508	15.494± .559	72–132
5	Lot 2. 0 to 5 minutes after separation	59	29	107.660±1.296	14.780± .916	13.729± .868	76–132
6	Lot 2. Random sample.	200	30	184.100± .776	16.264± .548	8.834± .300	140–216
7	Lot 6. Age 0 to 19 minutes.	24	31	128.000±1.908	13.856±1.348	10.825±1.066	108–152
8	Lot 6. Age 18 to 28 minutes	49	33	143.348± .624	6.480± .440	4.521± .309	132–160
9	Lot 6. Age 35 to 45 minutes	25	35	149.920±1.012	7.512± .716	5.010± .479	132–160
10	Lot 6. Age 75 to 90 minutes	42	36	161.524±1.004	9.648± .712	5.974± .441	140–180
11	Lot 6. Age 0 to 90 minutes (sum of rows 7–10)	140	—	147.544± .824	14.464± .584	9.803± .399	128–180
12	Lot 6. Random sample.	100	51	184.680± .848	12.596± .600	6.821± .327	156–224
13	Lot 7. Age 0 to 19 minutes	39	32	134.256±1.663	15.394±1.176	11.468± .857	108–160
14	Lots 6 and 7. All 0 to 19 (sum of rows 7 and 13)	63	—	131.872±1.288	15.176± .912	11.507± .701	108–160
15	Lots 6 and 8. Age 18 to 28 minutes (sum of row 7, and of 57 of another lot)	106	34	143.82 ± .544	8.296± .384	5.769± .268	112–168
16	Lot 9. Age 3 to 4 hours	93	37	149.636± .688	9.856± .488	6.587± .327	132–176
17	Lot 9. Age 4.20 to 5 hours	95	38	186.736± .652	9.416± .460	5.043± .247	164–216
18	Lot 9. Age 3 to 5 hours (sum of rows 16 and 17)	188	—	168.384±1.028	20.904± .727	12.415± .438	132–216
19	Lot 9. Random sample.	195	7	176.124±1.128	23.360± .797	13.262± .461	104–220
20	Lot 10. Age 12 hours	73	39	188.988± .996	12.612± .704	6.672± .374	136–216
21	Lot 10. Age 12 hours (same as row 20, but omitting .2 smallest).	71	39	190.424± .752	9.388± .531	4.930± .280	164–216
22	Lot 10. Age 18 hours	105	40	199.048± .380	11.844± .552	5.949± .278	168–228
23	Lot 3. Age 24 hours	300	41	168.532± .419	10.768± .629	6.389± .175	140–200
24	Lot 3. Early fission, depth of constriction less than ¼ breadth	42	44	167.620± .996	9.564± .704	5.706± .421	152–192
25	Lot 1. Early fission, constriction 4μ or less	131	13	175.696± .556	9.432± .393	5.368± .224	156–240

TABLE X.—*Continued.*

Comparison with Random Samples. (Each "Lot" consists of specimens with those of Table VIII. are numbered the same as in Table VIII. The headed "Table" gives the number of a table found in the appendix or

Breadth.				Mean Index, Ratio of Breadth to Length. Per Cent.	Coefficient of Correlation.
Mean in Microns.	Standard Deviation in Microns.	Coefficient of Variation.	Range of Variation in Microns.		
55.480±.297	5.040±.210	9.082±.382	44–72	63.136	.6546±.0337
49.540±.215	4.296±.152	8.671±.309	40–68	53.592	—.0938±.0496
50.220±.308	6.468±.218	12.877±.441	36–72	25.114	.6064±.0302
48.852±.210	4.216±.149	8.633±.307	36–64	54.080	—.3625±.0433
46.372±.332	3.804±.236	8.200±.524	36–56	44.037	—.3138±.0792
46.020±.251	5.256±.177	11.421±.390	36–60	25.084	.4282±.0389
60.168±.788	5.712±.556	9.495±.933	52–76	47.573	—.0337±.1375
54.284±.364	3.788±.260	6.976±.478	48–64	37.921	.1937±.0927
55.840±.636	4.724±.452	8.461±.813	48–64	37.296	.2799±.1243
54.192±.600	5.752±.424	10.617±.790	40–68	33.558	.5232±.0756
55.544±.308	5.416±.220	9.748±.397	40–76	38.038	—.0844±.0566
64.880±.580	8.624±.412	13.292±.645	44–88	35.131	.6469±.0392
46.768±.408	3.792±.288	8.108±.623	36–52	35.616	—.2546±.1010
51.872±.680	7.980±.480	15.382±.946	36–76	40.028	—.2476±.0798
50.832±.320	4.900±.228	9.640±.451	36–64	35.438	.1319±.0644
51.568±.322	4.752±.236	9.212±.459	40–64	34.546	.3201±.0628
60.168±.360	5.224±.256	8.679±.428	52–76	32.225	.5557±.0478
55.916±.324	6.588±.229	11.785±.416	40–76	33.372	.7132±.0242
47.364±.344	7.132±.244	15.057±.526	32–72	27.153	.3945±.0408
62.796±.464	5.872±.328	9.350±.526	48–80	33.275	.4868±.0602
63.156±.443	5.536±.313	8.763±.500	48–80	33.197	.3474±.0704
56.496±.292	4.428±.108	7.837±.367	48–68	28.427	.4304±.0536
40.320±.230	5.892±.162	14.615±.411	28–56	23.899	.5496±.0272
65.716±.706	6.784±.499	10.322±.768	48–80	39.286	.2215±.0999
55.480±.207	5.040+.210	9.082±.382	44–72	31.568	.6546±.0337

TABLE X.—*Continued.*

Row.	A. *Progeny of D (Caudatum Form).*	Number of Individuals.	Table.	Length.			
				Mean in Microns.	Standard Deviation in Microns.	Coefficient of Variation.	Range of Variation in Microns.
26	Lot 1. Fission, all stages but earliest	182	62	186.066± .710	14.208±.502	7.636±.271	160–224
27	Lot 1. Random sample	200	14	199.960± .740	15.528±.524	7.765±.263	148–240
28	Lot 1. Largest specimens of random sample, all more than 196 long	134	—	208.268± .566	9.720±.400		196–240
29	Lot 1. Combination of early fission with largest of random sample (sum of rows 25 and 28)	264	—	192.108	18.904		
30	Lot 2. Early stages of fission	40	44	165.200± .936	8.788±.664	5.320±.402	152–192
31	Lot 2. All stages of fission	62	42	171.548±1.188	13.848±.840	8.072±.492	144–212
32	Lot 2. Random sample	200	30	184.100± .776	16.264±.548	8.834±.300	140–216
	B. *Progeny of c (aurelia form).*						
33	Lot 4. Early fission, depth of constriction less than ¼ breadth	66	47	103.737± .650	7.823±.379	7.541±.445	83.3–126.7
34	Lot 4. Later stages of fission	53	63	121.383±1.053	11.367±.743	9.365±.613	100–156.7
35	Lot 4. Random sample	225	49	114.163± .784	17.443±.555	15.279±.497	73.3–160
36	Lot 5. Early fission	38	48	113.333± .850	7.778±.603	6.862±.533	93.3–126.7
37	Lot 5. Random sample	100	50	114.033± .820	12.140±.580	10.643±.513	86.7–146.7
38	Lots 4 and 5. All in early fission (sum of rows 33 and 36)	104	—	107.243± .600	9.070±.423	8.459±.398	83.3–126.7

of separation of the two halves). The measurements of these 59 young specimens are given in Table XXIX., while the polygon of variation for length appears at *b*, Diagram 4. For control, Table XXX. gives the measurements of a random sample of the culture from which these young specimens were selected. The constants deduced from the measurements of the young and of the random sample are shown in Table X., rows 4 to 6.

The following are the important facts which result from the examination of the young, in comparison with the adults (rows 5 and 6, Table X.).

1. The mean length of the young (0 to 5 minutes old) is considerably more than half that of the culture as a whole, being 107.660 microns as compared with 184.100 microns. Of course, the culture

TABLE X.—*Continued.*

Breadth.				Mean Index, Ratio of Breadth to Length. Per Cent.	Coefficient of Correlation.
Mean in Microns.	Standard Deviation in Microns.	Coefficient of Variation.	Range of Variation in Microns.		
49.540±.215	4.296±.152	8.671±.309	40–68	26.796	—.0938±.0496
50.220±.308	6.468±.218	12.877±.441	36–72	25.114	.6064±.0302
52.360±.348	5.964±.246		40–72		.4681±.0455
53.908	5.752				.0350±.0415
50.700±.364	3.432±.260	6.769±.513	48–80	30.765	.1048±.1055
50.388±.308	3.584±.216	7.111±.433	40–60	29.583	—.1136±.0840
46.020±.251	5.256±.177	11.421±.390	36–60	25.084	.4282±.0389
34.850±.287	3.453±.203	9.911±.587	26.7–43.3	33.623	.6502±.0479
34.590±.383	4.147±.273	11.989±.797	26.7–46.7	28.648	.3100±.0837
34.207±.241	5.363±.171	15.683±.511	20–50	30.177	.6757±.0244
45.263±.597	5.463±.423	12.071±.947	33.3–56.7	39.903	.6744±.0597
47.300±.437	6.490±.310	13.720±.667	36.7–66.7	41.455	.8152±.0226
38.653±.437	6.607±.310	17.089±.029	26.7–56.7		.7476±.0292

as a whole contains a large number of young specimens, so that the mean of the adults would be greater than that of the random sample.

2. The mean breadth of the young is almost exactly the same as that of the culture as a whole.

3. The relative variation in length is much greater for the young than for the culture as a whole, the coefficient being 13.729 for the former as compared with 8. 834 for the latter. Moreover, the coefficient of variation is almost three times as great as in the very youngest stages before separation (Table X., row 1), or in the first stages of fission (Table X., rows 25, 30, 33, 36).

This great variability of the young at this age indicates that they are growing rapidly in length; those five minutes old are considerably longer than those that have just separated, so that when all are taken

together the variation is great in proportion to the mean length. While the statistical data are themselves open to other interpretations, observation of the changes in living individuals, as described earlier, shows that this explanation is the correct one.

The *absolute* variation of the young, as shown by the standard deviation, is less, as might be expected, than that of the culture as a whole, though the difference is not great.

4. The variation in breadth, both absolute and relative, is less in the young than in the culture as a whole. The fact that it is still considerable perhaps indicates that changes in breadth are taking place during growth. To this we shall return immediately.

5. The correlation between length and breadth is negative in the young, while in the culture as a whole it is positive. In the former the coefficient is —.3138; in the latter it is + .4282.

The fact that the correlation is negative in young specimens (greater length associated with less breadth) indicates that while the animals are growing in length they are becoming more slender. With an increase of 10 microns in length the decrease in breadth is .757 micron. If we group together the unseparated halves (124 in number) with the separated ones (59), we find that the negative correlation between length and breadth is still greater, becoming —.3625 (see row 4, Table X.).

6. The mean ratio of breadth to length ("mean index") is much greater in the young than in the random sample. In the former the breadth is 44.037 per cent. of the length; in the latter but 25.084 per cent. If we include the unseparated halves with those under five minutes old, the breadth is 54.080 per cent. of the length (row 4, Table X.), while in the unseparated halves alone it is 59.166 per cent., and in the earliest stages of the unseparated halves it is 61.530 per cent. (see Table VIII., rows 4 and 5). There is thus a steady reduction of the ratio of breadth to length; to this is due the negative correlation of the two, when those of different ages are thrown together.

(*d*) *Age 0 to 19 Minutes* (*Tables XXXI. and XXXII.*).—From another culture composed of descendants of the individual *D*, specimens were taken on June 14 and kept to several different ages. The

various ages and measurements are given, with those of a random sample of the culture in lot 6, Table X.

The first set taken consisted of but 24 specimens, aged from 0 to 19 minutes. Though the number is small it is worth while to work out the constants for comparison with other stages in this same culture; it must be remembered that it is extremely difficult to get large numbers at any one time of individuals so young. The measurements are given in Table XXXI., while the constants are shown in row 7, Table X. For comparison with these a second lot of the same age, but containing 39 specimens, was taken from the same culture two weeks later. The measurements are given in Table XXXII.; the constants in row 13, Table X. The constants for the two sets taken together (63 specimens aged 0 to 19 minutes) are given in row 14, Table X.

Comparing these with the specimens but 0 to 5 minutes old, we find that the mean length has increased by 36 to 40 microns. The breadth is about the same in one of the lots (row 13, Table X.), but is much greater in the other (row 7). This difference is due to environmental effects. The coefficient of variability in length shows a decided decrease, indicating that growth is relatively more rapid during the first five minutes than later. The correlation between length and breadth is, as might be expected, negative in the sets 0 to 19 minutes old, as it was in the set still younger.

A number of specimens were killed at precisely known ages, and the measurements taken. Thus, from lot 7 (row 13, Table X.) a typical pair of young at the moment of separation measured 110×52 microns. At the age of one minute the two members of a pair measured each 124×52 microns; at two minutes another pair were each 120×52 microns. At three minutes one member of a pair measured 120×48 microns, the other 124×44. At five minutes the lengths of the two resulting from a certain fission were respectively 124×48 and 112×44 microns. Five specimens kept till they were precisely nineteen minutes old measured respectively 160×48 microns; 160×44; 152×36; 152×40; 156×44. The mean dimensions were thus 156×42.4 microns.

Outlines of individuals from 0 to 19 minutes old, showing the

relative sizes, are given in Fig. 4. These may be compared with the adults of this race, *a* to *c*, Fig. 1.

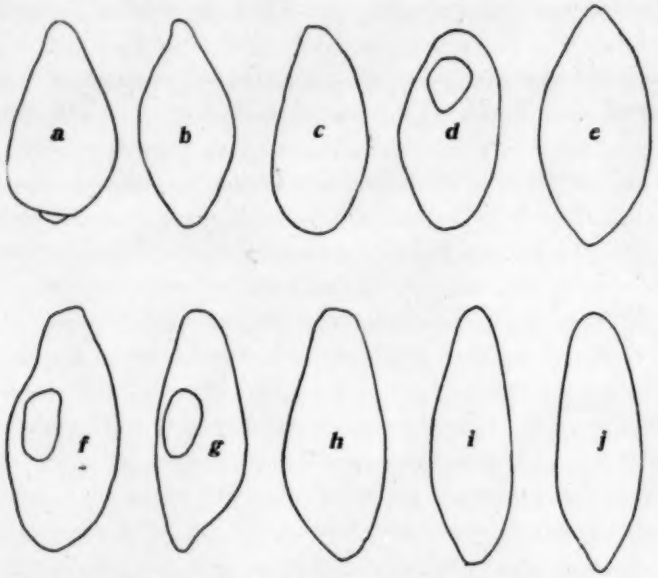

FIG. 4. Young *Paramecia*, descendants of *D* (*caudatum* form), from immediately after separation to the age of 19 minutes. *a* has just separated; *b*, *c* and *d* are two to three minutes old; *i* and *j* are 19 minutes old; the others are intermediate. These should be compared with the adults *a* to *c* of Fig. 1 (page 403), which are drawn to the same scale. All × 235.

(*e*) *Age 18 to 28 Minutes* (*Tables XXXIII. and XXXIV.*).—The first lot of this age (row 8, Table X.) contained 49 specimens (Table XXXIII.) and came on the same day from the same lot as the first lot of 24 of the preceding stage, so that the two are strictly comparable. The mean length has increased in the period of about thirteen minutes by nearly 16 microns, while the mean breadth has decreased 7 to 8 microns. The ratio of breadth to length has decreased almost 10 per cent. The correlation between length and breadth is in the present lot positive though small (.1937). If we should throw together the two lots (rows 7 and 8, Table X.), the correlation would, of course, be decidedly negative.

A second lot of 57 specimens aged 18 to 28 minutes was taken from the same culture about two weeks later. If we throw the two

lots together (Table XXXIV.) we have 106 specimens at this age (row 15, Table X.); the mean length is 143.82 microns, the mean breadth 50.832 microns, while the mean ratio of length to breadth is 35.438 per cent.

The polygon for variation in length at this age is shown at *c*, Diagram 4, p. 440.

(*f*) *Age 35 to 45 Minutes* (*Table XXXV.*).—From the same lot 6 (Table X.) from which came the first sets aged 0 to 19 and 18 to 28 minutes, there were taken on the same day 25 specimens that were allowed to reach the age of 35 to 45 minutes (row 9, Table X.). Growth has now become much slower. These specimens average 17 minutes older than the last set, yet they have increased in length only about 6.5 microns. The breadth remains about the same; the slight increase shown in the figures is probably not significant, since it disappears at the next stage. The mean ratio of breadth to length continues to decrease, reaching now 37.296 per cent. The correlation between length and breadth is more strongly positive than before (.2799), indicating that these dimensions are not changing so decidedly in opposite ways.

The polygon for variation in length at this age is shown at *d*, Diagram 4.

(*g*) *Age 75 to 90 Minutes* (*Table XXXVI.*).—Forty-two specimens of this age were measured, taken on the same day from the same lot from which came the sets last described (lot 6, Table X.). The specimens average about twice the age of those in the last set, the absolute increase being 45 minutes, yet the growth in length has been only about 12 microns, which is about the same as the growth in the first five minutes after separation. The breadth still remains about the same; it is notably less than in the very earliest stages. The ratio of breadth to length continues to decrease, reaching now 33.558 per cent. Meanwhile the correlation between length and breadth has increased greatly, till now, at .5232, it is not much below that of the culture as a whole (.6469).

(*h*) *Age 0 to 90 Minutes.*—From a single culture of *D*, on a single day, we have thus measured 140 young specimens, varying in age from 0 to 90 minutes. The constants for variability and correlation of such a collection are of interest; they are therefore given

in Table X., row 11. The variability, as measured by its coefficient, is less in both length and breadth than in the random sample, or in the collection of young specimens including only those under nineteen minutes in age. There is practically no correlation in the collection taken as a whole between length and breadth. This is because breadth at first decreases while length increases (giving negative correlation); later they increase together (giving positive correlation); the two tendencies about cancel each other in the collection as a whole.

Third Stage: Three to Five Hours Old (Tables XXXVII. and XXXVIII.).

Three days later than the sets shown in lot 6, Table X., and under as nearly the same conditions as possible, I took from the same culture of progeny of *D* two sets of young, keeping the first set till the age was between 3 and 4 hours, the second set till the age was between 4.20 and 5 hours (see lot 9, Table X.). The culture was, however, in a different condition from that of lot 6; it contained a very large number of young and dividing specimens. A random sample of this culture, containing 195 specimens, is shown in Table VII. (page 412), while the constants for this sample are shown in row 19, Table X. The entire left portion of Table VII., up to the length of about 160 microns, or more, evidently consists of young individuals in various stages of growth. This decreases the main length (176.124 microns) and the correlation (.3945), while it greatly increases the variability in length (13.262, as against 6.821 for the random sample of the previous lot).

(*i*) *Age 3 to 4 Hours (Table XXXVII.).*—The effects of different environmental conditions are at once seen on comparing this set of 93 specimens (Table X., row 16) with the set 75 to 90 minutes old, from the previous culture (Table X., row 10). The specimens of the present lot, though $1\frac{1}{4}$ to $2\frac{3}{4}$ hours older than the others, are shorter, the length (149.636 microns) being less by about 16 microns. The breadth is about the same as in the previous set; the correlation between the two is rather low (.3201).

(*j*) *Age 4.20 to 5 Hours (Table XXXVIII.).*—Ninety-five specimens kept for about an hour longer than those in the foregoing

set showed a rapid growth in length and breadth. The length now reaches 186.736 microns, the breadth 60.168; both dimensions are considerably greater than the mean of the random sample. Thus, the animals at this age had reached about the average size of the infusoria in a collection of the same descent taken at random. Table VI. (page 412) shows a sample of this same culture taken twenty-four hours earlier, at a time when little division was occurring; the mean length is very nearly the same as that of the young of the present set. The correlation between length and breadth has considerably increased.

Certain peculiar facts are brought out by considering these two sets together (Table X., row 18). Here we have a collection of 188 young individuals taken at practically the same time from a small watch-glass culture. The variability and correlation depend in a high degree on the length of time we keep these. If they are all kept three to four hours (row 16) or 4.20 to 5 hours (row 17), the variability in length is about 5 to 6, in breadth about 9. But when we keep part of them for the shorter period, part for the longer, the variability rises to about 12.5 for length and 12 for breadth. Again, the correlation between length and breadth is but .3201 and .5557 in the two lots taken separately, but when we take them together the correlation is much greater, rising to .7132. These relations show the important part which may be played by growth in determining observed variability and correlation; their significance will be taken up again in our general sections on these topics.

Fourth Stage: 12 to 18 Hours Old (Table X., Lot 10).

From the same culture of the progeny of *D* from which came the lots last described, but three days later were taken two lots of young, of 73 and 105 specimens, respectively, which were kept, the former to the age of 12 hours, the latter to the age of 18 hours.

(*k*) *Age 12 Hours (Table XXXIX., and rows 20 and 21, Table X.).*—There is a still further increase in both length and breadth, as compared with the specimens 4.20 to 5 hours old (see Table X., rows 20 and 21). Among the 73 specimens of this lot were two of about the same size which were much smaller than the others (see Table XXXIX.). There is little doubt, I believe, that these are the prod-

ucts of a second division; either one of the twelve-hour specimens had divided, or there was accidentally taken with them an older specimen which divided. In either case these two specimens do not belong in the twelve-hour lot, as they are much younger. On this account I have calculated the constants for this twelve-hour lot twice, once including these two small specimens (row 20, Table X.), the second time excluding them (row 21). The variability in length is much reduced—from 6.672 to 4.930—by the omission of these two. At the same time the correlation between length and breadth is likewise reduced from .4868 to .3474.

(1) *Age 18 Hours (Table XL., and row 22, Table X.).*—Growth in length continues, though very slowly; in six hours the increase has been less than during the first five minutes after separation. The animals at this age are decidedly longer than the mean for the culture as a whole, as judged from the random sample of Table VII. (page —), taken three days earlier. The mean breadth of the eighteen-hour specimens, while greater than that of the random sample, has decreased as compared with that of those only twelve hours old.

The variability of these two lots (12 and 18 hours old) of adult size is less than that of the random samples (for examples, rows 3, 6, 12, 19, Table X.).

Fifth Stage: 24 Hours Old (Table XLI., and row 23, Table X.).

A final lot of 300 specimens was selected while dividing and these were kept till they were 24 hours old. These were progeny of *D*, but were taken from the culture somewhat more than a month later than those 0 to 18 hours old. To understand their measurements it is necessary to take into consideration the cultural conditions. These animals were living in an ordinary hay culture, which was getting old, so that they were not dividing rapidly; they were rather slender in form. Now a large number of these was placed in a fresh decoction of hay and left there for 24 hours. They increased in size and began to divide rapidly. Now 150 dividing specimens (producing, of course, 300 young) were taken out and *returned to the original culture fluid*. This was for the purpose of preventing a second division before the end of the period of twenty-

four hours. As a result of this treatment they did not grow so rapidly as did the twelve- and eighteen-hour lots, and are smaller than these. The purpose in studying this group (as well as other groups) was mainly to determine the variability and the correlation between length and breadth. Both are less, as Table X. shows, than is usually the case in random samples.

The specimens 12, 18 and 24 hours old may be taken as types of adult *Paramecia* of this strain (progeny of *D*; *caudatum* form) before the changes leading to fission have begun.

Diagram 4 gives polygons of variation for the different ages, in descendants of *D*, as compared with a random sample; it shows clearly the part played in the observed variations by the presence of different stages of growth.

Sixth Stage: Preparing for Fission.

As Table X. shows, the adults of the progeny of *D* (*caudatum* form) reach a mean length of 168.532 to 199.048 microns (rows 23 and 22) under the cultural conditions employed, while the mean breadth varies from 40.320 (row 23) to 62.796 microns (row 20). But the *maximum* length is (under the same conditions), of course, much greater than the mean. In the random samples we find individuals up to 224 microns in length and 88 in breadth (see, for example, Table LI.); and among those 18 hours old (Table XL.) we find a length of 228 microns.

Now, when we compare these large adults with the specimens actually beginning fission (which are supposedly the oldest of all), certain peculiar facts appear. *The specimens beginning fission are by no means the longest of the lot;* a given culture contains many specimens much longer than those showing the first signs of division. Thus, in the "Lot 1" of Table VIII., we find 131 specimens in the very earliest stages of fission (Table XIII., page 442). The mean length of these is 175.696 microns (row 25, Table X.), and the longest specimen is 204 microns long. But in the random sample of the specimens that are not dividing, from this same lot (taken at the same time) the mean length is 199.960 microns (row 27, Table X.), and certain individuals reach a length of 240 microns (Table XIV., page 443). Of the two hundred specimens of the random

sample, 69, or more than one third, *are longer than the longest of the specimens beginning fission.* Only nine of the entire 200 falls below the mean length of the specimens beginning division.

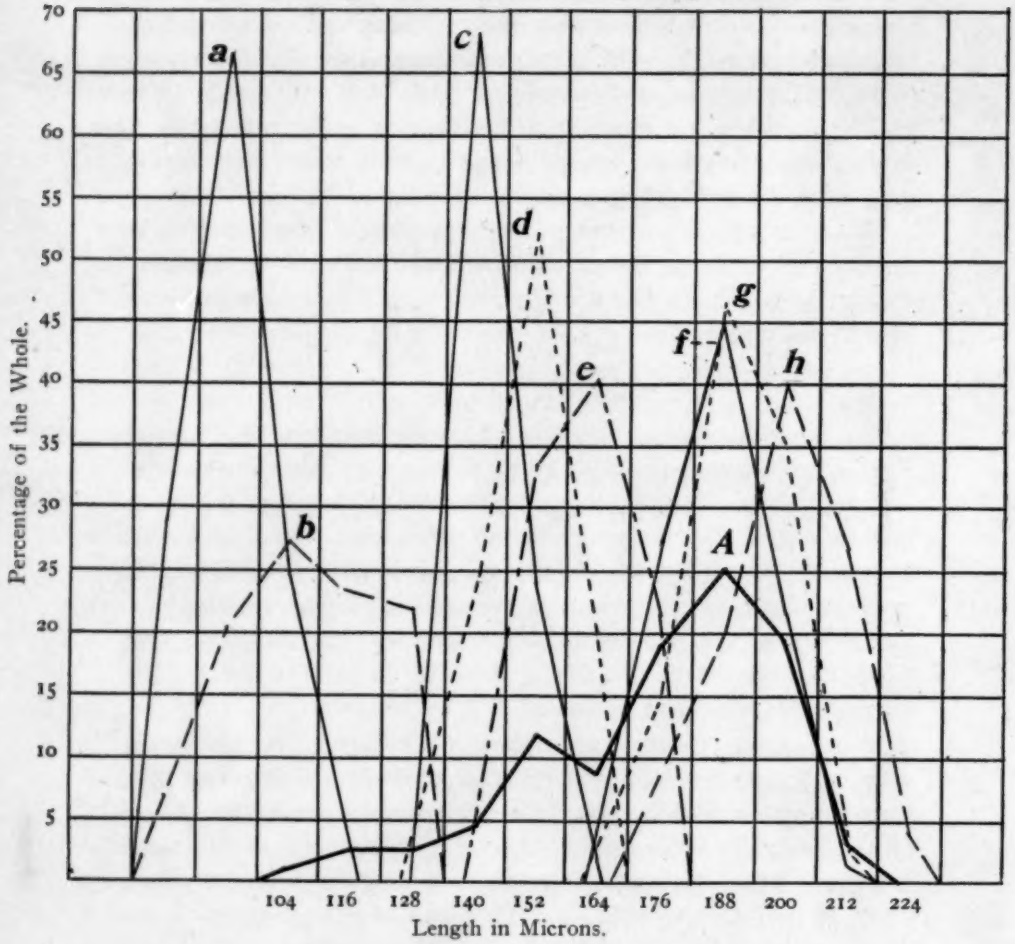

DIAGRAM 4. Polygons of variation in length for descendants of individual *D*, at various ages. *A* (heavy line), Random sample, 195 specimens (row 19, Table X.). *a*, youngest halves, constriction beginning (row 1, Table X.). *b*, age 0 to 5 minutes (row 5, Table X.). *c*, age 18 to 28 minutes (row 8, Table X.). *d*, age 35 to 45 minutes (row 9, Table X.). *e*, age 75 to 90 minutes (row 10, Table X.). *f*, age 4.20 to 5 hours (row 17, Table X.). *g*, age 12 hours (row 21, Table X.). *h*, age 18 hours (row 22, Table X.).

Since then the specimens beginning fission are not the longest of the culture, it is clear that *the length decreases before fission begins.* This is borne out by the form of the specimens beginning fission; though their mean length is less than that of the random sample, their mean breadth is greater (mean breadth 50.220 microns in the random sample, 55.480 in those beginning fission). While then the

TABLE XI.

Correlation Table for Depth of Constriction and Total Length in 313 Dividing Specimens from a Single Culture of Descendants of D.

All taken the same day.

Total Length of Body, in Microns.

Depth of Constriction in Microns.	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	
4	1	8	12	17	22	15	31	8	5	6	4	1	1						131
8		1	2	7	8	5	7	5	2										37
12			2	1	10	9	3	3				1				1			30
16				2	3	5	4	4	4	2	3	2							29
20			1	1		3	1	3	1	1	1								12
24		1						3	4	5	2		1						16
28					1		1	4	2	5	1	2	2	2	1	1			22
32				1		1				3	1	2	4	3	1	1			17
36									2		2	2	1		1	1		1	10
40											2		1	1		2	1	1	8
44																	1		1
	1	10	17	29	44	38	47	30	20	22	16	10	10	6	3	6	2	2	313

Length—Mean, 181.725 ± .512μ Depth of Constriction—Mean, 13.265μ
St. Dev., 13.446 ± .362μ St. Dev., 2.721μ
Coef. Var., 7.399 ± .201

Coef. of Cor. between Depth of Constriction and Length, .6882 ± .0201; Increase in Length for 1 unit of depth, .860μ; Coef. of Cor. if first row is omitted, .7818 ± .0194.

length decreases preparatory to fission, the breadth increases at the same time. How long before fission this change of dimensions begins I can see no way of determining. The period may perhaps be one or two hours.

Thus, the longest individuals of the culture are the adults that have not begun the changes preparatory to fission. These decrease in length and increase in breadth before fission.

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TABLE XII.

Correlation Table for Depth of Constriction and Breadth of Body, in 313 Dividing Specimens from a Single Culture of Descendants of D.

(Same lot shown in Tables XI., XIII. and LXII.)

Depth of Constriction in Microns.	Breadth in Microns.									
	40	44	48	52	56	60	64	68	72	
4		2	19	27	47	22	11	2	1	131
8		1	13	18	3	2				37
12		3	13	9	3	1		1		30
16	1	2	15	4	4	3				29
20	1	1	3	7						12
24		4	5	5	2					16
28		7	9	3	3					22
32	1	6	7	1	2					17
36	2	2	4	2						10
40		4	1	2	1					8
44			1							1
	5	32	90	78	65	28	11	3	1	313

Breadth—Mean, 52.026 ± .209μ Depth of Constriction—Mean, 13.265μ
St. Dev., 5.473 ± .148μ St. Dev., 2.721μ
Coef. Var., 10.544 ± .287

Coef. of Cor. between Depth of Constriction and Breadth, —.5232 ± .0277; Decrease in Breadth with Increase of 10μ in Depth, 2.630μ.

Omitting uppermost row: Coef. of Cor., —.3316 ± .0445μ; Decrease in Breadth with Increase of 10μ in Depth, 1.252μ.

TABLE XIII.

Correlation Table for Length and Breadth of 131 Specimens of Lot 1 in the Earliest Stages of Fission. (Descendants of D, Table X., row 25.)

Breadth in Microns.	Length in Microns.													
	156	160	164	168	172	176	180	184	188	192	196	200	204	
44		1		1										2
48	1	3	6	3	4	1		1						19
52		1	2	8	6	2	6	1	1					27
56		3	2	4	10	7	15	2	2	1	1			47
60			2	1	1	5	8	1	1	2	1			22
64					1		2	3	1	2	2			11
68										1		1		2
72													1	1
	1	8	12	17	22	15	31	8	5	6	4	1	1	131

Length—Mean, 175.696 ± .556μ Breadth—Mean, 55.480 ± .297μ
St. Dev., 9.432 ± .393μ St. Dev., 5.040 ± .210μ
Coef. Var., 5.368 ± .224 Coef. Var., 9.082 ± .382

Mean Index, 31.568 per cent.; Coef. Cor., .6546 ± .0337.

Seventh Stage: Fission.

Some of the data bearing on the dimensions during fission have been incidentally taken up in the account of the young in the earliest stages, before the two halves have separated.

(*m*) *Beginning Fission.* Descendants of *D* (*caudatum* Form). —Four lots of dividing specimens descended from the individual *D* were studied. These lots were taken at different times; the first included 313 dividing specimens (Tables XI. and XII., and rows 25–29, Table X.); the second 62 (Tables XLII., XLIII. (appendix) and rows 30–32, Table X.); the third 77 (Table XLIV., and rows 23–24, Table X.); the fourth 37. The dimensions of random samples of the same lots are given in Table X.

The large lot containing 313 dividing specimens may be described as typical; the others show the same relations, except as hereafter noted.

TABLE XIV.

Correlation Table for Random Sample of Specimens not Dividing, of Lot 1 (from which came the dividing specimens of Table XIII.). (See Table X., row 27.)

Length in Microns.

Breadth in Microns.	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	228	232	236	240	
36	1							1		2															4
40		1			1	2				1	3	1		2		1			2	1					12
44	1		2					1	3	5	4	10	5	4	4	2		2	1						44
48						1		1	1	1	5	3	7	4	2	4	3	3	2		1				38
52									2	2	2	5	6	6	7	7	3	4	2	1					47
56											2	2	1	11	2	3	3	1	4	3	1				33
60												1			2	1	2	4	3	1					14
64														1					1	2	1			1	6
68																									0
72																		1						1	2
	2	1	2	0	1	3	0	3	6	11	16	22	19	28	17	18	11	15	13	7	3	0	0	2	200

Length—Mean, 199.960 ± .740μ Breadth—Mean, 50.220 ± .308μ
St. Dev., 15.528 ± .524μ St. Dev., 6.468 ± .218μ
Coef. Var., 7.765 ± .263 Coef. Var., 12.877 ± .441
Mean Index, 25.114 per cent.; Coef. Cor., .6064 ± .0302.

In the dividing specimens the length of the body increases as the depth of the constriction between the two halves becomes greater; this is well shown in Fig. 2, page 416. In order to include only the earliest stages of fission we shall, of course, have to take the speci-

mens in which constriction is beginning. Among the 313 dividing specimens of lot 1 (Table XI.) there were 131 in which the depth of the constriction below the body surface was less than one unit of the micrometer scale (less than 4 microns). These may be taken as representing the earliest stages of fission. The depth of the constriction is in these specimens less than one twelfth the breadth. Their measurements are given in Table XIII., while the constants deduced from the measurements are shown in row 25, Table X. These should be compared with the measurements and constants for the random sample of the specimens not dividing in this same culture (Table XIV., and row 27, Table X.).

Examination of these tables shows the following remarkable facts:

1. The mean length of the specimens beginning fission (175.696 microns) is much *less* than the mean length of the random sample (199.960 microns)—although the latter must contain many specimens that have not reached adult size.

2. The range of variation in length is much less in the specimens beginning fission than in the culture as a whole. In those beginning division the range is from 156 to 204 microns; in the random sample it is from 148 to 240 microns.

3. The longest specimens beginning fission are 36 microns shorter than the longest of the random sample. In the random sample, 34.5 per cent. of all the specimens are longer than the longest of those beginning fission, while 95.5 per cent. are longer than the mean length of the specimens beginning fission.

4. The variation in length is decidedly less in the specimens beginning fission than in the random sample. In the lot beginning fission the coefficient of variation is but 5.368, while in the random sample it is 7.636.

It may here be noticed that coefficient of variation in the specimens beginning fission is less than that for conjugating specimens. as studied by Pearl (1907). To this matter we shall return later.

5. In the specimens beginning fission the mean breadth (55.480 microns) is greater than the mean breadth of the random sample (50.220 microns).

6. The variation in breadth is much less in the specimens begin-

ning fission than in the others. In the former the coefficient is but 9.082, while in the latter it is 12.877.

7. The mean index, or ratio of breadth to length, is much greater in the specimens beginning fission; in these it is 31.568 per cent., as contrasted with 25.114 per cent. in the random sample.

8. The correlation between length and breadth is high in the specimens beginning fission; it is somewhat greater than in the random sample. In the former it is .6546; in the latter .6064.

Owing to the smaller numbers in the other lots of dividing specimens, I included in the group "beginning fission" all those in which the depth of the constriction below the body surface was less than one fourth the breadth of the animal. Thus, all specimens with constriction 12 microns deep, or less, were included. Of course, these groups contained specimens in decidedly more advanced stages of fission than in the large group we have been considering. The numbers of specimens in early stages of fission thus secured were respectively 40 (Table XLIII.) and 42 (Table XLIV.). The constants for these, in comparison with random samples or adults, are shown in Table X. (rows 24 and 30).

As the tables show, these manifest in most particulars the same relations which we have brought out above for the larger and more precise set containing 131 specimens. The differences between the dividing specimens and the other individuals (as shown by the random samples, etc.) are in the main somewhat less in amount than in our first example. This is because in the smaller lots specimens are included in which lengthening and narrowing had begun, causing the dimensions to approach those of the specimens not dividing.

The most striking difference between our large lot (Table X., row 25) and the smaller ones (Table X., rows 24 and 30) is in the correlation between length and breadth. While in the larger lot the correlation was high, in the smaller ones it is small or quite lacking. This is again due to the inclusion of more advanced stages in the smaller lots; as the length increases the breadth decreases, tending to destroy the correlation.

Descendants of *c* (*aurelia* Form).—Two lots of dividing specimens were examined from the descendants of the small individual *c*. The first contained 119 specimens (Table XLV.); the second 63

specimens (Table XLVI.).[5] Selecting from these, as representing the early stages of fission, all those in which the depth of constriction is less than one fourth the diameter of the body, we obtain from the larger lot 66 specimens (Table XLVII.); from the smaller lot 38 specimens (Table XLVIII.). The constants for these, in comparison with those for random samples, are given in Table X. (lots 4 and 5, rows 33 to 38). The measurements of the random samples are shown in Tables XLIX. and L.

These specimens of the *aurelia* form show the same relations that are found in the *caudatum* form, with one exception. In lot 5 (Table X., row 36) the mean breadth of the specimens beginning fission is *less* than that of the random sample, instead of greater as in all other cases. But this peculiarity is due to environmental conditions. In lot 5 the breadth was very great in proportion to the length, as is shown by the dimensions of the random sample (Table L., and row 37, Table X.). In this lot the breadth was 41.555 per cent. of the length, while in most cases it is near to 30 per cent. This was due to the recent transference of the animals to a nutritive solution; they became very plump. Evidently, when preparing to divide the body tends to return to a constant form; in this case, therefore, it becomes narrower instead of broader.

In the specimens of the *aurelia* form, as in the *caudatum* form, all dimensions are less variable in the specimens beginning fission. This difference in variability, as compared with the random samples, is very great in some cases. Thus, while the coefficients of variation in length for the random samples of lots 4 and 5 are 15.279 and 10.643, for those of the same lots beginning fission they are but 7.541 and 6.862, respectively. Had we included in the lots beginning fission only specimens in which the depth of constriction was still less, the coefficients of variation would have been still smaller.

The constants for all specimens of *c* that are beginning fission, taken together, are shown in row 38, Table X. The standard deviations and coefficients of variation are, of course, greater than for

[5] In making these measurements of descendants of *c*, a higher power of the microscope was used, so that the single unit of measurement was $3\frac{1}{3}$ microns. This caused the tables (in the appendix) to take a somewhat different appearance from those of the descendants of *D*.

each of the two component lots taken separately, since the two lots differed as a result of different environmental conditions.

(*n*) *Later Stages of Fission.*—As the constriction deepens the animal as a whole becomes more elongated, while the breadth decreases slightly. These relations are shown both for the descendants of *D* (*caudatum* form) and the descendants of *c* (*aurelia* form) in Table X. (rows 25 and 26; 30 and 31; 33 and 34). In the large lot 1 of dividing descendants of *D*, comprising 313 specimens (Table XI.) the correlation between length of body and depth of constriction below the surface is .6882. The length increases 8.6 microns with every increase of 10 microns in the depth of constriction. The correlation between breadth and depth of constriction (Table XII.) is —.5232, the breadth decreasing 2.63 microns for each 10 microns increase in depth of constriction. If we include only the specimens in which lengthening has decidedly begun (thus omitting the earliest stages, in the uppermost rows of Tables XI. and XII.), then the correlation between length and depth of constriction is .7818; between breadth and depth of constriction, —.3316. With an increase of 10 microns in depth of constriction the length now increases 11.195 microns, while the breadth decreases 1.252 microns. In this same culture while the mean length of the 131 specimens beginning fission is 175.696 microns, that of the seven specimens having a connecting portion but 4 microns wide is 212.572 microns. Thus, the increase in length before separation takes place is 36.876 microns, or about 21 per cent. of the length at the time fission begins. The breadth has decreased from 55.480 microns at the beginning of fission to 43.428 microns in the seven specimens with the narrowest connections—a decrease of about 21 per cent. The ratio of breadth to length decreases from 31.568 per cent. at the beginning of fission to 20.430 per cent. just before separation.

Corresponding relations are shown in other lots of dividing specimens; some of the data are given in Table X.

2. Summary on Growth in Paramecium with a Growth Curve.

We have thus followed the growth from the time when the individual is but half a constricting specimen to the period when it is again ready to separate into two new individuals. We are ready,

therefore, to outline the main features of the growth of *Paramecium*, and to construct curves which shall give an idea of the processes involved. In spite of an incredible amount of work devoted to collecting the data, certain of the less important features of the growth curves must remain obscure, but the main facts are clear.

The main outlines of the changes due to growth are as follows: From the time the constriction appears in the mother until a few minutes after separation takes place, the length increases rapidly, while the breadth decreases a little. A few minutes after separation the processes become less rapid. The breadth soon reaches its minimum, then begins to increase like the length, though more slowly. Growth in length continues for at least eighteen hours; the time undoubtedly varies with the conditions. The breadth continues to increase for some time, but it undergoes marked fluctuations, due to environmental conditions. In lot 10 (Table X.) it decreased between the ages of 12 and 18 hours; this is probably an environmental effect, not one due to the normal growth processes.

As the time for fission approaches the animals are considerably more than twice as long as the original halves from which they developed. Now as fission comes on they shorten and thicken, all tending to approach a uniform length and thickness. There is thus much less variation in the dimensions at the beginning of fission than in specimens taken at random. Now the constriction appears and the animal begins to narrow and extend in the way already described, finally separating into two parts.

If from our data we construct curves showing these changes, we get such results as are shown in Diagram 5.

Method of Constructing the Curves.—The horizontal scale represents the time in hours, while the vertical scale represents the measurements of the animals in microns. The upper curve shows the length, the lower one breadth, as measured from the base line. Fission is assumed to take place once in twenty-four hours, which is an approximation to a rate commonly occurring. The time between the appearance of the constriction and the actual separation of the two halves is taken as one half hour.

The relative distances of the two curves from the base line shows the relative dimensions of length and breadth. The vertical rise of

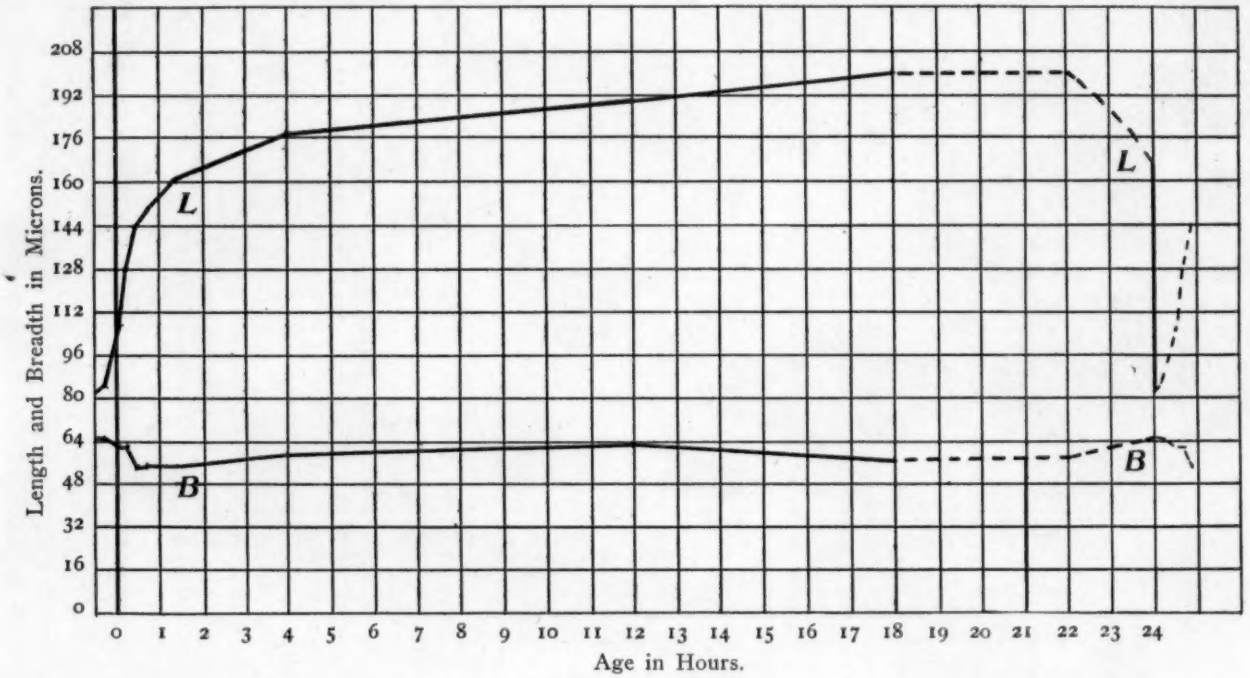

DIAGRAM 5. Curves of growth, for length and breadth in *Paramecium* plotted directly from Table XV., page 451. The upper line marked *L* is the curve of length; the lower line (*B*) that for breadth. The horizontal scale represents the time in hours; the vertical scale gives the measurements in microns. The relative distances of the two curves from the base line *o* shows the proportions of length and breadth at the different ages. The vertical rise of the curve shows the proportion of growth to the original length. The distance from the base line to the curve is 357 times the actual dimensions at the given ages. Fission occurs at *o* and at 24 hours. The curves are not smoothed. The broken parts of the curves are not constructed from precise data.

the curve of length shows the actual proportion of growth to the original length. The distance from the base to the curves is 357 times the actual dimension at the given time.

In order to show changes due to growth alone all the data for such a curve should be measurements from a single uniform culture on a single day; otherwise environmental differences complicate the matter, as we shall see more clearly in the next division of this paper. Now, it is impracticable to obtain from a single culture on a single day measurements of all the required stages. We are compelled therefore to make certain corrections in some of the measurements, to compensate so far as we can for environmental differences. As Table X. shows, the mean dimensions of random samples differ much in (for examples) lots 1 (row 3) and 6 (row 12). It will not do, therefore, to compare *directly* the young of these two lots. Since we have from lot 6 the greatest number of different stages, it is best to make the measurements from this the basis for the curve, correcting others, so far as possible, to compare with this. In lot 2 the mean length (Table X., row 6) is almost exactly the same as for lot 6, so that we may use the measurements of lot 2 without correction, so far as length is concerned. On this account we shall employ lot 2 for the earliest stages, in place of lot 1, though the latter is based on a larger number of specimens.

Since the mean breadth of the sample of lot 6 is 64.880 microns, while that of lot 2 is but 46.020 microns, it is necessary to correct the breadth for lot 2. At first thought it would seem that the proper method of making this correction would be by multiplying the breadths of the different sets of lot 2 by the ratio 64.880/46.020. This would be the proper method of procedure if we were dealing with the same stages of growth in the two lots; the specimens of lot 2 would be made plump, like those of lot 6. But the stage with which we are dealing is that of the beginning of fission. Now, we have already seen that when the specimens not dividing are plump, the breadth does not increase at the approach of fission nearly so much as when the specimens not dividing are thin. Indeed, if the specimens are very plump, there is an actual decrease, instead of an increase, at the approach of fission. Our problem is: What would be the breadth of specimens beginning fission, in which the length is 82.600, and the animals are very plump, as in lot 6? This problem can best be solved by asking what is the ratio of breadth to length in specimens beginning fission, in a very plump culture? In lot 3 (row 7, Table VIII.) we have such a plump culture, and we find that the ratio of breadth to length is, in the earliest stage of fission, 78.563 per cent. We therefore take this as the ratio of breadth to length for the earliest stage of lot 2, from which the corrected breadth is found to be 64.893. If this decreases at the same relative rate as actually occurred in lot 2, then the breadth 15 minutes after the beginning of constriction would be 64.493 microns.

We are compelled to use, further, lots 9 and 10 (Table X.). In lot 9 both length and breadth require correction to make them comparable with the measurements of lot 6. The correction is made by multiplying the

dimensions by the ratio between the length of the random samples of the two lots. In lot 9 we use only the average of the two sets, as given in row 18, Table X.

In lot 10, since we unfortunately have no random sample, we are unable to make a correction.

Owing to the very great difference in the environmental conditions of lot 3 (rows 23 and 24, Table X.) we are unable to use the 24-hour-old specimens of that lot, although we need measurements at that age. The older portions of the curve (beyond 18 hours, at the right) cannot be plotted from exact data, and there are certain features of much importance for which it appears that the collection of such data would be almost impossible. As we have shown, before fission the animals shorten and thicken. How long before fission this begins it is not possible to say; in making the curve the period is arbitrarily taken as two hours.

When we make the corrections above described, we have the following mean dimensions at different ages, as data for the construction of our curve. The *ages* given are the *average* ages for the lots considered; thus the age for row 8, Table X. (18 to 28 minutes) is taken as 23 minutes.

TABLE XV.

Dimensions in Microns of Paramecia (Descendants of D) at Different Ages, Corrected (so far as possible) to Correspond with Those of Lot 6, Table X. Data used in making the Curves of Growth.

Age.	Lot.	Mean Length in Microns.	Mean Breadth in Microns.
Beginning constriction	Row 4, Table VIII.	82.600	64.893
Fifteen minutes after beginning constriction	" 5, " VIII.	85.774	64.493
2½ minutes after separation	" 5, " X.	107.660	59.355
9½ minutes	" 7, " X.	128.000	60.168
23 minutes	" 8, " X.	143.348	54.284
40 minutes	" 9, " X.	149.920	55.840
82½ minutes	" 10, " X.	161.524	54.192
4 hours	" 18, " X.	176.560	58.922
12 hours	" 20, " X.	188.988	62.796
18 hours	" 22, " X.	199.048	56.496
Beginning constriction	" 30, " X.	165.200	64.893

When we lay off on the vertical scale the distances corresponding to the lengths and breadths at the different periods, as given in the above table, and connect these points, we obtain the curves given in Diagram 5.

Characteristics of the Curves.—As the curves show, the length increases with great rapidity for about twenty minutes after fission; continues less rapidly for about an hour, and still less rapidly for four or five hours. Now the increase continues, though very slowly, till a maximum is reached at a length considerably greater than twice the original length; later the length decreases in preparation for

fission; this decrease continues till the length is just twice the original length. Now the constriction appears, so that the animal may be looked on as two; the length, therefore, drops in a straight line to the original length found at the beginning of the curve. The breadth decreases from the beginning till about an hour after fission; then slowly increases; it shows in the course of the twenty-four hours many fluctuations which are doubtless mainly due to differences in the environment—especially to differences in the amount of food taken. In preparation for fission the breadth increases at the same time that the length decreases.

The curve of length is much the more interesting of the two, since it is the one which represents mainly the actual growth. It is of great interest to find that this curve of growth in a single cell is of essentially the same form and character as those which have been obtained for the growth of many higher organisms, composed of many cells. A number of such curves are brought together in the recent interesting paper of Robertson (1908). Inspection shows at once that the curve of growth in *Parmecium* closely resembles that for growth of the rat, as worked out by Donaldson (1906); for growth of man, and for growth in various other organisms.

The curve of growth, as is well known, is a logarithmic curve in the cases where it has been worked out mathematically. While the growth in *Paramecium* has merely been plotted empirically, it is evident that it is essentially a similar logarithmic curve; this could doubtless be worked out from the data given.

The fact that the curve of growth is essentially the same in the unicellular organism as in the animal composed of millions of cells is in some respects surprising. In the brain of the rat, or in its body, the curve of growth is the resultant of the growth of many different groups of cells, some groups growing at one period, some at another; yet the resultant curves are of the same character as when there is growth in but a single cell.

The temporal relations shown in the curves are likewise of much interest. As our diagram shows, that portion of the curve showing the greatest curvature requires in *Paramecium* about four hours from the beginning. In the rat the corresponding part of the curve takes several months, while in man it requires several years. It

seems extraordinary that a process following the same laws should in some cases be measured by hours, in other cases by months, in others by years.

3. Effects of Growth on the Observed Variation.

A random sample of an ordinary culture of *Paramecium* contains specimens falling in all parts of the growth curves represented in Diagram 5. If we measure the various members of such a sample, as was done by Pearl (1907), we shall then find many variations in size, which variations consist to a considerable extent of different growth stages. Not all the observed variations are due to this factor, but its importance is very considerable. This will best be appreciated by running through the columns headed "coefficients of variation" in Table X. If we take samples including specimens falling in the early parts of the growth curve, when the absolute size is small but the changes with growth are very marked, then the coefficients of variation in length are high; thus in rows 4 and 5 they are 15.494 and 13.729, respectively, while in the random sample of the same culture the coefficient is but 8.834 (row 6). On the other hand, if we take specimens restricted to a very small portion of the curve, the coefficient of variation becomes very low; thus in a lot whose age falls between 18 and 28 minutes the variation is but 4.521 (row 8); at the age of 4.20 to 5 hours is 5.043 (row 17), though the variation for a random sample of this same culture is 13.262 (row 19). The effects of growth on variation are shown to the eye in Diagram 4, p. 440.

Variation at Fission.—The effects of growth on the observed variation are likewise seen when we compare random samples with individuals that are at a definite stage in the life history. Thus, if we take specimens at the beginning of fission, when the constriction first appears, we find the coefficient of variation very low, as compared with those of random samples of the same cultures. This is readily seen in the following tabulation of the coefficients of variation for the four cultures of Table X. in which the specimens beginning fission were studied (see next page).

Variation in Conjugants.—Again, the same thing appears when we compare conjugating individuals with random samples of the

same cultures. Conjugation does not occur till a certain stage of growth has been reached, and the conjugants do not include specimens undergoing the changes preparatory to fission. The conjugants would then fall in those portions of the growth curve that are nearly straight; that is, there would be in these little variation due to growth.

TABLE XVI.

Coefficients of Variation.

Lot.	Length.		Breadth.	
	Beginning Fission.	Random Sample.	Beginning Fission.	Random Sample.
1	5.368	7.765	9.082	12.877
2	5.320	8.834	6.769	11.421
4	7.541	15.279	9.911	15.683
5	6.862	10.643	12.071	13.720

Pearl (1907) has already shown that the observed variability of conjugants is less than that of random samples of the same culture. I have made extensive studies of conjugants and find the same thing. Details regarding the relation of conjugation to variation and heredity are to be taken up in a later communication; here I give merely the coefficients of variation for certain cases, as compared with those of random samples.

TABLE XVII.

Coefficients of Variation for Conjugants, as compared with those for random samples of non-conjugants of the same culture.

Lot.	Length.		Breadth.	
	Conjugants.	Non-Conjugants.	Conjugants.	Non-Conjugants.
A, Pearl.	6.668	8.185	9.398	11.112
C, "	7.439	9.123	7.910	10.894
a, Jennings.	7.39	11.578	12.409	19.176
b, "	7.678	11.026	15.766	18.142

On comparing the coefficients of variation in conjugants, as given in Table XVII., with those for specimens beginning fission (Table XVI.), and those for specimens at definite ages (Table X.), it is found that in the conjugants the variation is not so small as it is in specimens at definite growth stages. This shows clearly that nothing is required to explain the low variation of conjugants, save the fact that a certain number of growth stages (the earlier and later ones)

are lacking in these. There is no evidence of an unusually low degree of congenital variation in the conjugants, for the non-conjugating specimens beginning fission show a still lower variability (Table XVI.).

It appears highly probable that if we could examine a large number of individuals, derived from the same parent, cultivated under identically the same conditions, and all in precisely the same stage of growth, we should find coefficients of variation considerably smaller than the smallest we have found, which is 4.521 (row 8, Table X.). Indeed, if we could further exclude all inaccuracies of measurement, it is quite possible that the coefficient of variation would approach closely to zero, if it did not reach it completely. This would, of course, mean that the variations observed among the progeny of a single individual are not congenital, but are all due to growth and environmental action. Further evidence of this will come out later in this paper.

4. Effects of Growth on the Observed Correlation Between Length and Breadth.

As Diagram 5 shows, the curves of length and breadth diverge at the beginning, then run for a considerable distance nearly parallel, then finally approach each other. That is, at first the breadth decreases while the length increases; later they increase together; and still later the breadth increases while the length decreases. If a collection of specimens includes individuals in various different stages of growth (as is usually the case), then these various relations of breadth to length will deeply affect the amount of correlation observed between the two dimensions.

Thus, if we take a collection composed of various ages under one hour, when the length is increasing while the breadth is decreasing, then on the whole greater length will be associated with less breadth, so that the correlation between them will tend to be negative. This is the explanation of the negative correlation shown in Table X., rows 2, 4, 5, 7, 11, 13, 14. Next follows a period (from about the end of the first hour to the fourth) in which the inclusion of individuals of different ages tends to cause a certain degree of positive correlation, since the two dimensions are increasing together. Then

comes a long period in which both dimensions remain nearly the same—the length increasing slowly, while the breadth fluctuates. Different growth stages during this period have little marked effect on the coefficient of correlation between length and breadth; they tend to prevent its reaching 1.000, but this it would not reach for other reasons.

Now, for a certain period before fission (taken as two hours, in our curves), the length decreases while the breadth increases. Greater breadth will then be associated with less length, tending to produce again a negative correlation. If we make a collection of individuals representing various stages in this process, we should, therefore, expect to find the correlation much less than in collections taken (1) either before these processes have begun, or (2) after they are ended. We can realize this, in the main, by taking from a large random sample all the largest specimens (which are, of course, the older ones) and combining these into a single correlation table with specimens from the same culture that are beginning fission (the *oldest* specimens of the culture). I performed this operation for lot 1 of Table X. This collection contains 131 specimens beginning fission (row 25, Table X.), and 134 specimens (not dividing) that are 196 microns, or more, in length (row 28, Table X.); throwing these together, we have a collection of 264 of the oldest specimens in the culture (row 29, Table X.). For the 131 specimens beginning fission the coefficient of correlation is + .6546; for the 134 large specimens it is + .4681. When the two are taken together the correlation disappears. The computation gives us a coefficient of + .0350, but this is less than its probable error (.0415), so that the figures have no significance; no correlation appears.

The effects of the inclusion of various growth stages on the observed correlation shows itself in many other ways, which will become evident to anyone who carefully examines the data of Table X., in connection with our curves of growth (Diagram 5), and the relations brought out in the foregoing paragraphs. Note, for example, the coefficients of correlation for lot 9 (rows 16–18, Table X.). For the specimens 3 to 4 hours old the coefficient is but .3201, and for those 4.20 to 5 hours old it is .5557. When we throw these two lots together, so as to include a much greater proportion of the

growth curve, the correlation rises to .7132. In this larger collection the short specimens are much the narrower, the large specimens much broader—giving high positive correlation. Slight changes in one dimension may not be accompanied by notable changes in the other, while *great* changes in one are always accompanied by changes in the other. This is a relation which we shall meet again.

While thus growth has a very great effect on the correlation to be computed from the measurements of a collection of *Paramecia*, it is important to bear in mind the fact that it is by no means the only factor concerned in correlation. This becomes evident as soon as we take a collection in which the specimens are all in nearly the same stage of growth; the coefficient of correlation is then high. This is perhaps best realized by considering specimens in the beginning of fission. As we have before noticed, in the collection of 131 specimens beginning fission, from lot 1, great pains were taken to include only a single stage in the process. This collection gives a high positive correlation of .6546. This correlation can be due only to the fact that in specimens at a single growth stage the length and breadth tend to bear a certain proportion to each other. The effects of this are clearly seen in many other collections of Table X. Thus, in rows 8, 9 and 15 the specimens all fall in the period when length is increasing while breadth is decreasing; yet there is in each case a small positive correlation. This is due to the fact that the period of growth over which each collection extended was small, so that the negative correlation due to growth was more than counterbalanced by the inherent proportionality of length to breadth. A collection including only specimens that were all in the same stage of growth would undoubtedly (other things begin equal) show a high correlation between length and breadth, no matter what point on the growth curves they represented. This signifies, of course, that in any given stage of growth the relation of length to breadth tends to be the same in all specimens—although in *different* stages of growth this is often not the case. Other factors which modify the correlation will be considered in the later sections of this paper; a summary of all these factors will be presented in a special section.

With this we conclude our study of growth in *Paramecium;*

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being prepared to understand the part played by this in the observed variations and correlations, we may pass to other factors affecting these.

IV. THE EFFECTS OF ENVIRONMENTAL CONDITIONS ON DIMENSIONS, VARIATION AND CORRELATION.

The data for the study of growth, just concluded, show incidentally that environmental conditions affect profoundly the dimensions, variation and correlation in *Paramecium*. As we have seen, samples taken from the same culture on two successive days are not strictly comparable for determining matters relating to growth, because of the environmental changes from day to day, inducing marked changes in the organisms. Thus, in a given culture we found that the mean length at the age of 1¼ to 1½ hours was 161.524 microns; three days later specimens more than twice as old, from the same culture, were smaller, measuring but 149.636 microns. We wish now to investigate the causes of such differences.

We shall not attempt at present a systematic investigation of the effects of different chemical and physical agents on size, form and variation, though this is a matter which much needs study. Our present object is rather to examine the effects of altered nutritional conditions and of the commoner "favorable" and "unfavorable" conditions. We shall study the variations from the standpoint of interest in the organism rather than in the agents inducing them, the purpose being to form a conception of the changes which may be looked for in *Paramecium* as a result of common alterations, mainly nutritional, in its cultural conditions. One of the results of this study will be to show that we cannot assign a definite effect to each agent taken in any absolute way. What effect a given agent will have depends on the previous condition of the organisms on which it acts. The same agent produces at one time an increase in size, at another a decrease; at one time it increases the variability; at another it decreases it. A given agent may either increase the positive correlation between length and breadth, or it may decrease it or convert it into a negative correlation. In succeeding days the same agent may produce these diverse effects on the same set of *Paramecia*.

Yet, of course, these results are not produced haphazard; what we wish to study are the laws they follow.

The effects of the environment were studied mainly on the same animals that served for the study of growth. Two strains were used; one consisted of descendants of the individual *D*, of the *caudatum* form, the other of descendants of *c* (*aurelia* form). The results show the extent of the variations producible through environmental action in the progeny of single individuals multiplying by fission. No conjugation occurred in the *D* strain during the time it was under experimentation. On a given date, therefore, the age of the individuals, as measured in generations of the "cycle," was about the same.

Table XVIII. gives a summary of the statistical results in the experiments on the effects of the environment; it will be referred to frequently in the following account (see next page).

1. Progeny of *D* (*caudatum* Form).

The individual *D* was isolated April 12, 1907; it measured, as nearly as could be determined when alive, about 250 microns. It was placed in culture fluid made of boiled hay and the progeny were kept in such cultures for months. Characteristic progeny of *D* are shown in Fig. 1, *a* to *d*.

The experiments with the descendants of *D* may be divided into three series.

First Series.

Old Large Culture.—On June 11 a sample of 100 of the descendants of *D* was killed, from a hay culture that had stood several weeks and was flourishing, though multiplication was not occurring actively. This culture was in a vessel about nine inches across. The measurements of this sample are given in Table V. (page 406), while the constants are found in row 1, Table XVIII.

Effects of Fresh Hay Infusion.—Three days after these measurements were taken, a number of individuals of this culture were removed and placed in a fresh hay infusion, in a watch-glass; in this they were allowed to remain 24 hours. The increased food in the fresh infusion caused them to increase much in breadth (from 49.000 microns to 64.880 microns), and at the same time to begin to

TABLE XVIII.

Effects of Environmental Conditions on Dimensions and Constants of Varia-

same culture at the same time (except in rows 12, 15 and 20). The appendix or elsewhere, in which fuller data are given for the lot in

Row.	A. *Progeny of D. First Series.*	Number of Individuals.	Table.	Length.			
				Mean in Microns.	Standard Deviation in Microns.	Coefficient of Variation.	Range of Variation in Microns.
1	Random sample of *D*, June 11, 1907	100	5	188.360± .980	14.532± .692	7.715±.370	128–228
2	Same after 24 hours in fresh hay infusion, June 15	100	51	184.680± .848	12.596± .600	6.821±.327	156–224
3	Two days after last; culture fluid not renewed, June 17	135	6	185.008± .836	14.420± .592	7.794±.324	148–212
4	Same, after 24 hours in fresh hay infusion. Rapid multiplication, June 18	195	7	176.124±1.128	23.360± .797	13.262±.461	104–220
5	Same, one week later; bacteria multiplied injuriously, June 25	178	52	201.888±1.147	22.680± .811	11.233±.407	140–256
6	Starvation, same as row 2, but left 11 days in small quantity of fluid, June 25	100	53	149.360± .736	10.896± .520	7.296±.350	128–188
	Second Series.						
7	24 hours in fresh hay infusion; rapid multiplication, July 17	200	30	1 .10 0 .776	16.264± .548	8.834±.300	140–216
8	Same as last, but starved a week, July 24	150	19	146.108± .563	10.228± .398	7.003±.274	120–176
9	Same as last, but 24 hours in fresh hay infusion, July 25	350	20	163.932± .754	20.928± .533	12.767±.331	120–220
10	Same as last, but kept 1 week without change of fluid, July 31	150	21	174.400± .819	14.876± .579	8.530±.335	132–212
11	Same as last, but kept 48 hours in fresh hay infusion, Aug. 3	150	22	191.360± .943	17.116± .666	8.945±.351	136–240
12	Rows 8, 10 and 11 combined	450	—	180.624± .748	23.537± .529	13.795±.316	120–240
	Third Series.						
13	Slender, old culture, in large jar, September 15	100	54	202.280±1.031	15.284± .729	7.556±.362	160–232
14	Same as last, after 48 hours in fresh hay infusion, September 15	100	55	175.320±1.060	15.708± .749	8.959±.431	124–216
15	Rows 13 and 14, combined	200	—	188.800± .980	20.540±1.092	10.879±.371	124–232
	B. *Progeny of c.*						
16	Random sample of *c*, June 11, 1907	100	4	130.120± .628	9.284± .443	7.134±.342	104–156
17	Random sample of *c*, August 9	100	56	123.666± .813	12.040± .573	9.736±.469	100–160

TABLE XVIII.—*Continued.*

tion in Paramecium. Each row consists of specimens taken from the column headed "Table" gives the number of a table found in the question.

Breadth.				Mean Index, or Ratio of Breadth to Length. Per Cent.	Coefficient of Correlation.
Mean in Microns.	Standard Deviation in Microns.	Coefficient of Variation.	Range of Variation in Microns.		
49.000±.548	8.144±.388	16.618± .814	28–76	26.029	.4188±.0556
64.880±.580	8.624±.412	13.292± .645	44–88	35.131	.6469±.0392
43.556±.392	6.748±.276	15.490± .651	32–60	23.517	.5955±.0375
47.364±.344	7.132±.244	15.057± .526	32–72	27.153	.3945±.0408
56.112±.395	7.808±.279	13.913± .507	36–80	27.850	.6771±.0274
38.080±.356	5.288±.252	13.881± .675	28–52	25.515	.4481±.0539
46.020±.251	5.256±.177	11.421± .390	36–60	25.084	.4282±.0389
31.180±.212	3.881±.151	12.473± .493	20–40	21.337	.3906±.0467
46.684±.488	13.484±.344	28.879± .793	20–80	28.236	.8463±.0102
44.800±.429	7.796±.304	17.397± .698	32–68	25.657	.5704±.0372
54.880±.431	7.824±.305	14.255± .566	36–84	28.639	.7364±.0252
43.600±.377	11.852±.266	27.184± .654	20–84		
49.600±.298	4.412±.210	8.896± .428	40–60	24.593	.4085±.0562
63.160±.472	7.000±.334	11.083± .535	44–80	36.123	.5376±.0480
56.380±.427	8.956±.302	15.884± .549	40–80	30.350	—.2613±.0414
36.280±.260	3.880±.184	10.700± .516	28–44	27.913	.5208±.0492
33.600±.400	5.917±.283	17.608± .865	23.3–50	27.136	.6258±.0410

TABLE XVIII.—*Continued.*

Row.	B. Progeny of *c*. Continued.	Number of Individuals.	Table.	Length			
				Mean in Microns.	Standard Deviation in Microns.	Coefficient of Variation.	Range of Variation in Microns.
18	Same as last, but 24 hours after addition of boiled grass, August 10	225	49	114.163± .784	17.443± .555	15.279±.497	73.3–160
19	Same as row 17, but 24 hours in fresh hay infusion, August 12	100	50	114.033± .820	12.140± .580	10.646±.513	86.7–146.7
20	Rows 17 and 19, together; same animals, half in old fluid, half in new	200	—	118.850± .622	13.037± .440	10.698±.374	86.7–160
21	Conjugating culture, large vessel, September 25	200	57	158.800± .877	18.384± .620	11.578±.396	124–200
22	Same culture, 5 days after, food getting scarce	100	58	129.640± .867	12.848± .613	9.911±.477	100–152
23	Large, old culture, January 23, 1908;	100	59	144.880±1.097	16.264± .776	11.224±.542	100–176
24	Same, two days later, January 25, 1908	50	—	130.640±1.227	12.863± .868	9.846±.670	104–156
25	Another old culture, January 23, 1908	100	—	137.200± .842	12.488± .596	9.102±.438	104–162
26	Same as row 23, but starved 3 weeks, February 14	37	—	102.594±1.161	10.467± .821	10.202±.808	76–128
27	Same as row 23, but cultivated in small watch glass, January 30–February 15, 1908	10_0	60	100.320± .528	7.828± .373	7.804±.374	76–120

multiply. The measurements of a sample of 100 of these are given in Table LI. (appendix), while the constants are found in row 2, Table XVIII. The increased breadth, with little change in the length, of course, results in an increase of the mean index or ratio of breadth to length; while in row 1 this was but 26.029 per cent., in the present lot it is 35.131 per cent. It is worthy of notice that with the increase in ratio of breadth to length there is an increase in the correlation between length and breadth from .4188 to .6469.

Scarcity of Food.—The watch-glass culture just described (row 2, Table XVIII.) was now allowed to stand for three days (till June 17) without renewing the culture fluid. The animals had multiplied greatly, so that food became scarce; as a result they became thin. The measurements are given in Table VI. (page 412) and the constants in row 3, Table XVIII. While the length remained about the same, the mean thickness of the body decreased from 64.880 to 43.556 microns. The mean ratio of breadth to length fell from 35.131 per

TABLE XVIII.—*Continued.*

Breadth.				Mean Index or Ratio of Breadth to Length. Per Cent.	Coefficient of Correlation.
Mean in Microns.	Standard Deviation in Microns.	Coefficient of Variation.	Range of Variation in Microns.		
34.207±.241	5.363±.171	15.683± .511	20–50	30.177	.6757±.0244
47 300±.437	6.490±.310	13.720± .667	36.7–66.7	41.455	.8152±.0226
40.450±.441	9.247±.312	22.857± .810	23.3–66.7		.1758±.0462
38.560±.353	7.396±.249	19.176± .670	16–60	24.244	.7135±.0234
35.440±.400	5.928±.283	16.730± .820	20–48	27.262	.7576±.0287
54.160±.765	11.346±.541	20.948±1.042	32–84	37.106	.8500±.0187
37.760±.639	6.697±.452	17.736±1.233	28–52	28.975	.4141±.0790
37.960±.413	6.128±.292	16.142± .790	24–56	27.625	.6691±.0373
23.892±.644	5.804±.455	24.291±2.014	16–40	23.067	.8018±.0396
26.480±.266	3.944±.188	14.895± .753	16–36	26.321	.7671±.0278

cent. to 23.517 per cent., and at the same time correlation between the two fell from .6469 to .5955.

Thus, within a week we find enormous fluctuations in breadth, due to changes in the amount of food, while the length remains about the same. The breadth is much more affected by nutritional changes than is the length.

Rapid Multiplication.—To the watch-glass culture just described (row 3) new hay infusion was added. Twenty-four hours later (June 18) multiplication was occurring actively; stages of fission and all the stages of growth were numerous. Measurements of 195 specimens, taken at random at this time (Table VII., page 412, and row 4, Table XVIII.) show a very great increase in the range and amount of the variability in length, while there is little change in the breadth. This is, of course, due to the fact that the culture contains many young; these differ much from the adults in length, but little in breadth. The mean length decreases from 185.008 to 176.124

microns, and the variability in length almost doubles, increasing from 7.794 to 13.262. Owing to the inclusion of many young individuals, in which the length is increasing while the breadth is stationary or decreasing, the correlation between length and breadth decreases to .3945. Inspection of Tables VI. and VII. (page 412) shows at a glance the great effect of nutrition and division on the range and distribution of variations in size and form.

Injurious Bacteria.—A remarkable effect of what may be called "bad" conditions is shown in this series of experiments. The same watch-glass culture shown in row 3, Table XVIII., was allowed to stand for a week, till June 25. Bacteria of a certain character multiplied greatly, and seemed to get the upper hand of the *Paramecia*. The latter became opaque and abnormal in appearance, and some of them died, disintegrating into shapeless masses. It was now observed that many of the specimens still living were very large, and that variation in size was extreme. The distribution of the variations is shown in Table LII.; the constants in row 5, Table XVIII. Though no multiplication is occurring, so that no young are present, the range of variation is from 140 to 256 microns, while in row 3, from which this lot is derived, the range is only from 148 to 212 microns. The mean length has increased to 201.888 microns, one of the greatest mean lengths ever observed in progeny of *D*. The maximum size for descendants of *D* was likewise reached in this culture; in no other case were specimens 256 microns long observed.

Starvation.—In striking contrast with the effects of much nutrition (row 4, Table XVIII.) and of injurious bacteria (row 5) are the results of starvation (Table LIII., and row 6, Table XVIII.). The starving culture consisted of individuals from the same culture as row 1, placed in fresh hay infusion June 14. The constants before they were placed in the hay infusion are given in row 1, Table XVIII., while the immediate effects of the infusion are shown in row 2 of the same table. The same animals were left in this fluid for eleven days, till June 25. They had evidently begun to starve; they were small and thin and almost half of them had died. The dimensions are given in Table LIII., and the constants in row 6, Table XVIII. The length had fallen from 184.680 to 149.360 microns; the breadth from 64.880 to 38.080 microns. The breadth

decreases with lack of food proportionately more than does the length, so that the ratio of length to breadth has fallen from 35.131 per cent. to 25.515 per cent. It is to be noticed, however, that this greater proportionate decrease of breadth takes place in the first days after the withdrawal of abundant food, since after the animals had been only three days without new food the ratio of breadth to length fell to 23.517 per cent. (row 3, Table XVIII.); it did not decrease farther after starvation began.

A comparative inspection of Tables VII. (page 412) and LIII. (appendix) shows to the eye the very great effects of nutrition on size and variation.

Second Series.

After the series of experiments described above, the progeny of *D* were kept in large culture jars of hay and water for about three weeks. Then followed an exceedingly instructive series of experiments on the effects of environmental conditions, the results of which are shown in Tables XIX.–XXII. and in the large Table XVIII., rows 7 to 12. Mere inspection of the correlation tables shows the effects in such a striking way that I have placed the main tables together in the text, instead of relegating them to the appendix.

Fresh Hay Infusion.—On July 16, 1907, specimens from the large cultures were placed in a watch-glass of hay infusion and allowed to remain twenty-four hours. This induced rapid multiplication; while this was occurring a random sample of 200 specimens was measured, with the results shown in Table XXX. (appendix), and in row 7, Table XVIII.

Starvation.—Next these were allowed to starve for a week; then 150 specimens were measured (Table XIX., and row 8, Table XVIII.). The results may be compared with our other starving culture of Table LIII., and row 6, Table XVIII. It will be noticed that for both length and breadth the amount of variation is not great; that the absolute dimensions are small; that the ratio of breadth to length (21.337 per cent.) is the least we have even seen, and that the correlation between length and breadth is very low (.3906).

Effects of Abundant Food on a Starving Culture.—Now this starving culture (Table XIX.) was placed for twenty-four hours in

TABLE XIX.

Correlation Table for Length and Breadth of a Starving Culture of Descendants of D. (Row 8, Table XVIII.)

Length in Microns.

Breadth in Microns.	120	124	128	132	136	140	144	148	152	156	160	164	168	172	176	
20						1										1
24	1	1	1		1	2	2		1	1						10
28	1		6	2	5	12	10	3	9	4	2					54
32		1		4	3	8	1	8	11	9		2		1		48
36					2	3	3	7	1	8	3	1	1		1	30
40			1					3		1	1	1				7
	2	2	8	6	11	26	16	21	22	23	6	4	1	1	1	150

Length—Mean, 146.108 ± .563μ Breadth—Mean, 31.180 ± .212μ
St. Dev., 10.228 ± .398μ St. Dev., 3.881 ± .151μ
Coef. Var., 7.003 ± .274 Coef. Var., 12.473 ± .493

Mean Index or Ratio of Breadth to Length, 21.337 per cent.; Coef. Cor., .3906 ± .0467.

TABLE XX.

Correlation Table for Length and Breadth of Descendants of D when a Starving Culture (Table XIX.) is placed for 24 Hours in Fresh Hay Infusion. (Row 9, Table XVIII.)

Length in Microns.

Breadth in Microns.	120	124	128	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	
20		1			1																						2
24	3	1	1	1	5	4	1	2																			18
28	1	1	2	3	3	11	5	4	1	2	1																34
32			1	1	6	3	6	4	3	2		1															27
36			1	1	3	3	1	3	4	5		1															22
40			1		2		2	3	4	3	3	3	2	2	2												27
44				1		1	2	1	4	2	5	6	3	1			1										27
48					1		2		2	5	5	9	4	2	2	3	1		1	1							38
52							1	1	2	2	7	7	4	3	1	1	4	2	3								38
56									1	3	2	1	3	10	6	3	2	6	1	1							39
60								1		1		1	2	4	5	6	3	2	3	2		2					32
64													1	1	8	3	4	2	4							1	24
68																1		3	1	6		1		1			13
72														1	1		1	1					1				5
76															1			1			1						3
80																								1			1
	4	3	6	7	21	22	20	18	21	22	25	29	15	14	21	25	19	12	19	10	9	1	3	2	1	1	350

Length—Mean, 163.932 ± .754μ Breadth—Mean, 46.684 ± .488μ
St. Dev., 20.928 ± .533μ St. Dev., 13.484 ± .344μ
Coef. Var., 12.767 ± .331 Coef. Var., 28.879 ± .793

Mean Index, 28.236 per cent.; Coef. Cor., .8463 ± .0102.

TABLE XXI.

Correlation Table for Length and Breadth of Descendants of D, after Remaining One Week in Hay Infusion, Unchanged. (Row 10, Table XVIII.)

Length in Microns.

Breadth in Microns.	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	
32					1		1	3	2		1	1										9
36	1		2			3	2	4	3	3	1	2	1									22
40						1	4	2	3	3	2	10	2	2	1		1					31
44						2	1	1	2	7	5	5		1	2	1						27
48					1						3	2	3	4	3	1	2	4				23
52					1			1		2		4	2	1	2	2	1	1	2		1	20
56									1			1	2			1	3			1		9
60										1	1		1	2		1						6
64																						0
68												1						1	1			3
	1	0	2	0	3	6	8	11	11	16	13	26	11	10	8	6	7	6	3	1	1	150

Length—Mean, 174.400 ± .819μ Breadth—Mean, 44.800 ± .429μ
St. Dev., 14.876 ± .579μ St. Dev., 7.796 ± .304μ
Coef. Var., 8.530 ± .335 Coef. Var., 17.397 ± .698
Mean Index or Ratio of Breadth to Length, 25.657 per cent.; Coef. Cor., .5704 ± .0372.

TABLE XXII.

Correlation Table for Length and Breadth, after the Culture shown in Table XXI. has remained 48 hours in Fresh Hay Infusion.
(Row 11, Table XVIII.)

Length in Microns.

Breadth in Microns.	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	228	232	236	240	
36	1				2	1																						4
40				1					1	1																		3
44							1	1		1	1	3	1															8
48			1					1	4	2	3	2	7	3	1	1		1										26
52								1			3	3	2	5	8	3	1	1		2								29
56										1		2	2	4	1	8	1		2	6	1				1			29
60											1		1	1	4	3	4	3	3	2	1	1						24
64												1	2	1	1	3	3	1	3	1	1		1					18
68																1			1	1		1						4
72																			1	1	1	1						4
76																												0
80																												0
84																											1	1
	1	0	1	1	2	1	1	3	5	5	8	11	15	14	15	19	9	6	10	13	4	3	1	0	1	0	1	150

Length—Mean, 191.360 ± .943μ Breadth—Mean, 54.880 ± .431μ
St. Dev., 17.116 ± .666μ St. Dev., 7.824 ± .305μ
Coef. Var., 8.945 ± .351 Coef. Var., 14.255 ± .566
Mean Index, 28.639 per cent.; Coef Cor., 7364 ± .0252.

a fresh hay infusion. At once the culture "spread out" greatly, in a way that will appear on comparing Table XIX., for the starving culture, with Table XX., for those twenty-four hours in nutritive fluid. Many of the animals began to grow at once after they were placed in the nutritive fluid, so that the maximum length increased from 176 to 220 microns, the maximum breadth from 40 to 80 microns (see rows 8 and 9, Table XVIII.). Others had not yet begun to increase when the sample of Table XX. was taken, so that

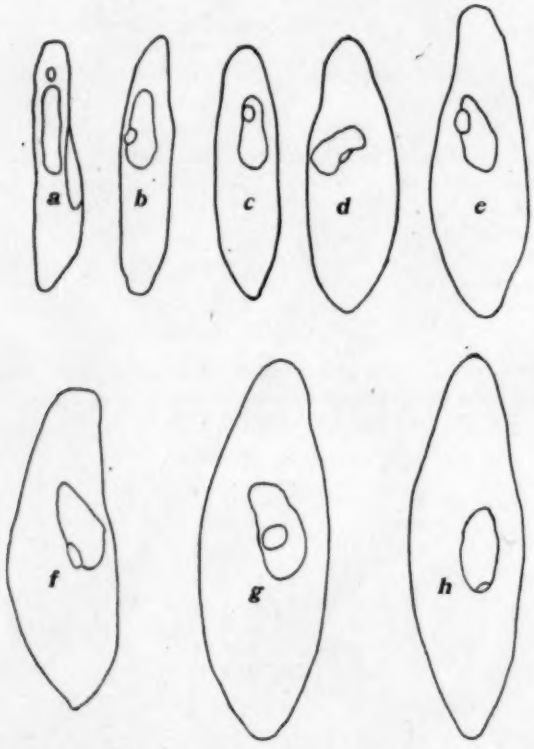

FIG. 5. Characteristic forms and sizes from a culture of descendants of *D* (*caudatum* form), that had been starved for a week (Table XIX.), then was left twenty-four hours in fresh hay infusion (Table XX.). *a* and *b*, Starved specimens. *c*, *d*, *e*, *f*, transitional forms, becoming large and plump in the abundant food; *g*, characteristic large, plump form. *a* to *g* from Table XX. *h*, characteristic form a week later (Table XXI.); animals becoming thinner again, but retaining the increased length. All × 235.

the minimum size remained as before; and between these extremes all intermediate gradations were found. Fig. 5 shows characteristic forms and sizes from this culture, *a* and *b* showing the starving condition, while *c* to *f* show various stages in the transition to the largest size, one of which is shown at *g*.

As a result of these changes, the variability has increased enormously. The coefficient of variation in length has increased in twenty-four hours from 7.003 to 12.767; that for breadth has more than doubled, increasing from 12.473 to 28.879. The mean size has likewise increased greatly, while the ratio of breadth to length has changed from 21.337 per cent. to 28.236 per cent. Perhaps the most striking change is in the correlation between length and breadth. In the starving culture this is but .3906; twenty-four hours later it has become, in the growing culture, .8463—one of the highest coefficients of correlation that I have ever found in *Paramecium*. It is evident that breadth and length are increasing proportionately, on the whole, so that the inclusion of different degrees of increase in size in Table XX. gives a high coefficient of correlation. Furthermore, the fact that fission had not begun in this lot permits the correlation to remain high; if there were many young included, the correlation would, of course, be lowered. With every increase of 10 microns in length the breadth increases 5.452 microns.

Fluid Unchanged for a Week.—Now the same culture was kept for a week in the same fluid. The animals had reached more nearly a condition of equilibrium; the variability, and with it the correlation, had greatly decreased, while the mean length had increased (Table XXI., and row 10, Table XVIII.). It is noticeable here, as in many other cases, that the coefficient of correlation decreases when the ratio of breadth to length decreases.

Forty-eight Hours in New Culture Fluid.—The addition of new hay infusion to the culture just described caused in forty-eight hours a considerable increase in mean length and breadth, while the variation did not change greatly (Table XXII., and row 11, Table XVIII.). Again, as the ratio of breadth to length increases, the correlation between the two likewise increases.

Résumé.—Polygons showing the changes in the animals of this series, from the starving condition of Table XIX. to the well-fed

condition of Table XXII. are given in Diagram 6; these, taken in connection with Fig. 5 and with Tables XIX. to XXII. give a good idea of the changes in dimensions and variation that may be pro-

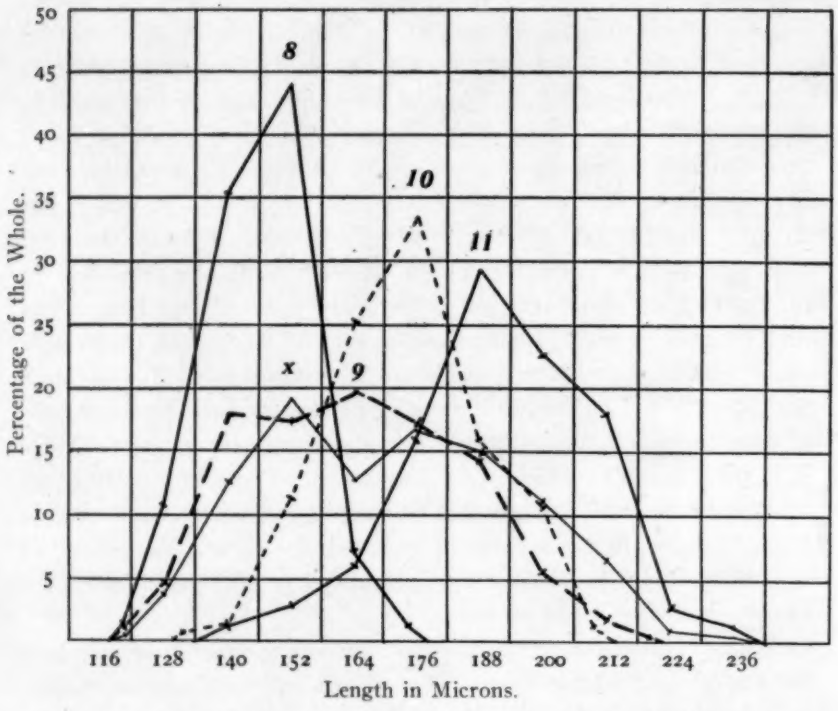

DIAGRAM 6. Polygons of variation in length for a culture of descendants of the individual *D* when subjected successively to varied conditions of nutrition. The numbers above the highest points of the polygons correspond to rows of Table XVIII., in which are given the constants for the different polygons. *8*, culture starved a week. *9* (heavy broken line), same as 8, but after 24 hours in fresh hay infusion. *10*, same after one week in the same fluid, unchanged. *11*, same after 48 hours in fresh hay infusion. *x*, polygon for combination of 8, 10 and 11, showing its resemblance to the polygon for 9 alone.

The correlation tables for these polygons are numbers XIX. to XXII., pages 466, 467.

duced in a short time by changes in the conditions of nutrition. Evidently Table XX., taken twenty-four hours after the starving specimens were placed in the fresh hay infusion, is a transitional

condition, including representatives of the small, starving condition, the well grown condition, and intermediate states; it is a sort of a résumé of the variations due to nutrition. If we add together the tables given by the starving culture (earlier than Table XX.) and the two well-fed cultures (later than Table XX.), we get a collection of 450 individuals, in which the variation in length and breadth is about the same as for Table XX. (see row 12, Table XVIII.). For Table XX. the coefficients of variation for length and breadth are 12.767 and 28.879; the corresponding coefficients for the three lots combined are 13.795 and 27.184.

Although the animals are all descended from the same parent and have lived under the same conditions save for the ten days during which these experiments lasted, we find that in the period just mentioned the polygons of distribution of variations in length have so changed that the one for the end of the ten day period (11, Diagram 6) hardly more than overlaps at one end that for the beginning of the period (8, Diagram 6).

Addition of fresh hay infusion causes in these cases an increase in length, in breadth, in variation, and in the correlation between length and breadth. But whether these results shall follow depends upon the previous condition of the animals. This is illustrated by the fact that there is one exception to the statement just made; the variability in breadth decreased in place of increasing in the transition from Table XXI. to Table XXII. The effect of the previous condition is better seen in the experiments of the third series, to be described next.

Third Series.

A culture of the descendants of *D* was rather ill-fed, though not starving; the animals were long and slender (Fig. 6, *a* and *b*). Half of these were allowed to remain in the old fluid, while half were placed in fresh hay infusion. After forty-eight hours, a random sample of each set was measured. The measurements of the set in the old fluid are given in Table LIV., the constants in row 13, Table XVIII. The results of keeping the animals forty-eight hours in the fresh infusion are shown in Table LV., and in row 14, Table XVIII. The animals grew plump and multiplied; the mean breadth increased

from 49.600 microns to 63.160 microns (characteristic form shown at *c*, Fig. 6). But *the mean length decreased* from 202.280 to 175.320 microns. This is probably due to rapid multiplication; the animals now divide before they reach the length which they had at first. As a result of the increase in breadth and decrease in length, of course,

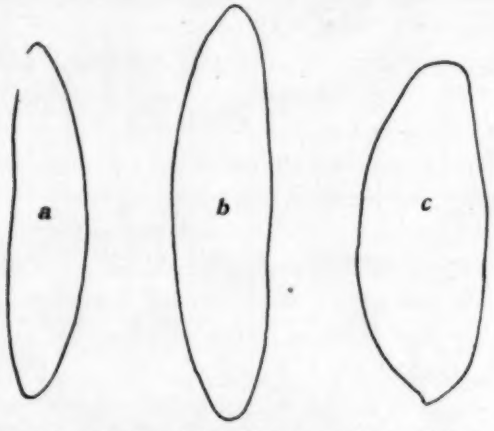

FIG. 6. *a* and *b*, characteristic slender specimens from row 13, Table XVIII. *c*, characteristic short plump specimen from row 14, Table XVIII.; produced by allowing those of row 13 to remain 24 hours in fresh hay infusion. Descendants of *D* (*caudatum* form). All × 235.

the mean ratio of breadth to length increased greatly, from 24.593 per cent. to 36.123 per cent. With the increase of this ratio, the correlation likewise increased, as is usually the case. The variation increased, both in breadth and in length.

These are the results if we consider separately the two samples, taken forty-eight hours apart. But if we throw them together, looking at them merely as a sample of the descendants of *D*, taken at intervals, we get a surprising effect on the correlation between length and breath. The marked positive correlation in the two samples taken separately *disappears and is replaced by a negative correlation.* In the first sample the correlation is + .4085; in the second it is + .5376; in the two together it is — .2613. (The constants for the two together are given in row 15, Table XVIII.) The negative correlation is, of course, due to the fact that the nutritive fluid causes the breadth to increase and the length to decrease, so that, on the

whole, when the two samples are taken together, greater breadth is associated with less length.

2. Progeny of *c* (*aurelia* Form).

With the smaller *Paramecia,* progeny of the small individual *c,* a similar series of experiments was undertaken. The individual *c* came from the same wild culture as *D;* its length, as nearly as could be determined in life, was 120 microns. It was isolated April 8, 1907. Fig. 3 shows some examples of the descendants of *c,* drawn to the same scale as the figures of the descendants of *D.*

Random Sample.—On June 11 one hundred of the progeny of *c* gave the measurements shown in Table IV., page 405, the constants being given in row 16, Table XVIII.

Effect of Adding Boiled Hay.—On August 9 a fairly flourishing culture of the descendants of *c* was examined, with the results shown in Table LVI., and in row 17, Table XVIII. To this culture a quantity of boiled grass was added; this caused rapid multiplication. Twenty-four hours later a sample of 225 specimens was measured, with the results shown in Table XLIX., and row 18, Table XVIII. The added nutrition has caused the mean length to decrease, while the mean breadth remains nearly the same. This is due to the fact that the main effect of the nutrition was to cause rapid multiplication rather than growth in size. The coefficient of variation in length increased greatly, from 9.736 to 15.279, while the variation in breadth remained about the same, though with a slight *decrease.* This peculiar result is mainly due to the fact that the culture after the addition of the grass (row 18) contains many young specimens, which differ from the adults greatly in length, but little in breadth. As usual, we find that an increase in the ratio of breadth to length is accompanied by an increase in the correlation between the two.

Effect of Fresh Hay Infusion.—The next day (August 11) another lot from the culture shown in Table LVI. (row 17, Table XVIII.) was placed in a fresh hay infusion and left twenty-four hours. This nutritive fluid caused the animals to become very plump, while at the same time a moderate amount of fission was induced. The results are shown in Table L., and in row 19, Table

XVIII. As there appears, the mean breadth increased from 33.600 to 47.300 microns. The length, on the other hand, decreased from 123.666 to 114.033 microns. The mean ratio of breadth to length thus increased very greatly, from 27.136 per cent. to 41.455 per cent. The latter is the largest mean index I have ever observed in *Paramecia* not selected with relation to the age of the individuals; it is exceeded only by the mean index of the young halves during fission (see Table X.). With the increase in the mean ratio of breadth to length, there is as usual an increase in the correlation between the two dimensions; this reaches the unusually high value of .8152. The nutritive fluid left the variation in length about the same, but considerably decreased the variation in breadth. This is undoubtedly due to the fact that before the hay infusion was introduced some of the specimens were well fed, some poorly fed, as the chances of the daily life determined; while after the infusion was introduced *all* were well fed, so that there was less variation in breadth than before. Characteristic forms after the infusion was introduced are shown in Fig. 3, *a* to *c* (page 423).

The facts in these cases are nearly parallel with those observed in the third series of experiments on the progeny of *D* (Table XVIII., rows 13–15). If we combine the two samples of *c* (row 20, Table XVIII.), as we did those of *D*, the effect is, as in the case of *D*, to decrease greatly the correlation between length and breadth But in the present case the very high positive correlation of the two samples taken separately is not entirely overcome by combining them, though the correlation falls to .1758. The actual numerical coefficient just given is the resultant of a number of conflicting factors. In the two samples taken separately greater length is associated on the whole with greater breadth, giving high positive correlation, which in passing from Table LVI. to Table L. an increase in breadth is associated with a decrease in length, tending to diminish the correlation. The facts show clearly that the observed statistical correlation does not involve any necessary and constant relation of the one dimension to the other; both dimensions depend on various factors, which sometimes act in the same way on both, sometimes differently.

Combining the two samples of *c* (as in row 20, Table XVIII.), gives, of course, increased variation, illustrating, like most of our

results, the fact that a definite coefficient of variation cannot be considered characteristic of a given species or race. The observed variation depends on many factors.

Conjugating Culture.—The progeny of *c* I divided into two sets, both of which were kept in larger culture vessels and maintained by adding boiled hay at intervals. September 25 one of these cultures was found to be undergoing an epidemic of conjugation (though, of course, all were progeny of a single individual). The details regarding the relation of conjugation to the phenomena we are studying are to be taken up in a later communication, but I will give here the essential facts regarding dimensions and constants of variation, in order that our picture of the changes undergone by the *c* line may be as complete as possible. A random sample of the non-conjugants of this conjugating culture gave the results shown in row 21, Table XVIII., and in Table LVII. The mean length (158.800 microns) was considerably greater than has been observed in any other culture of *c*. Whether this fact has any relation to the occurrence of conjugation, or whether it is merely a matter of the environmental conditions must remain for the present a question.

Scarcity of Food After Conjugation.—This conjugating culture was allowed to stand five days. All conjugation ceased and the food began to get scarce. Now a sample gave the results shown in row 22, Table XVIII., and in Table LVIII. The length had decreased from 158.800 to 129.640 microns. Breadth likewise decreased, though not in so great a proportion as length, so that the ratio of breadth to length increased. As is usual when this ratio increases, the coefficient of correlation likewise increased.

Variation in Different Divisions of the Same Pure Line on the Same Date.—After the observations just described, the two cultures composed of the progeny of *c* were maintained for several months. On January 23, 1908, samples from each were measured, giving the results shown in rows 23 and 25, Table XVIII. As is evident, the two differed considerably. The details do not demand attention, save that in one of these old cultures (row 23, and Table LIX.) the coefficient of correlation between length and breadth was the highest I have ever observed in *Paramecium,* reaching .8500. Both these cultures were flourishing and well fed.

Effects of Lack of Food.—From the culture shown in row 23, Table XVIII., a large number of specimens were removed and placed in a small watch-glass, which was allowed to stand for two days. The food decreased rapidly and the animals became smaller, giving the results shown in row 24, Table XVIII. The mean length had decreased 10.174 per cent.; the mean breadth 33.024 per cent. These were now allowed to stand for three weeks more in the watch-glass, without adding food. At the end of this time they were in the extremes of starvation, and only 37 specimens remained of the many hundreds originally present. These 37 gave the results shown in row 26, Table XVIII. As compared with the original condition of row 23, the mean length had decreased 30.638 per cent., the mean breadth 55.886 per cent. A peculiar fact is that this starving culture shows a very high coefficient of correlation between length and breadth (.8018), while in our other starving cultures this has not been the case (see rows 6 and 8, Table XVIII.).

From the culture of large specimens shown in row 23 another lot was removed January 30 and kept in a small watch-glass, new hay infusion being added at intervals. In spite of this addition of new food material, and the fact that they continued to flourish and multiply, these decreased in length even more than in the starving culture, the mean being 100.320. This is the smallest mean length observed in any lot of the *c* line. The data for this lot are given in row 27, Table XVIII., and in Table LX.

3. Summary on the Effects of Environment.

The facts given above show that the nature of the environment affects greatly the dimensions, proportions and variations of *Paramecium*, and that these effects are produced with great ease and rapidity by such changes as are common in any culture of these infusoria. Some of the more important effects may be summarized as follows:

Effect on Length.—Under the influence of varied nutritional conditions the *length* varies extremely. In the line descended from the individual *D* the mean length varied under different conditions from 146.108 to 202.280 microns—the difference being 38.445 per cent. of the smallest mean length. In the *c* line the variation in mean length

under the influence of the environment was from 100.320 to 158.800 microns, or 58.293 per cent. of the lowest mean. The *extreme* lengths in each line, of course, differed still more; in the *D* line the extreme variation in length was from 104 to 256 microns, or 146.153 per cent. of the least length; in the *c* line it was from 73.3 to 200 microns, or 172.851 per cent. of the minimal length.

Effect on Breadth.—The breadth (the thickness of the body) varies under different environmental conditions more readily and in a higher degree than does the length. In the *D* line the mean breadth varied in different cultures from 31.180 to 64.880 microns, or by 108.08 per cent. of the lowest mean; the *extreme* variation in breadth, under different conditions, was from 20 to 88 microns, or 340 per cent. of the minimal breadth. In the *c* line the mean breadth varied under different conditions from 23.892 to 54.160 microns, or by 126.69 per cent. of the lowest mean; the *extreme* variation in breadth was from 16 to 84 microns, or 425 per cent. of the minimal breadth. The greater variability of the breadth, as compared with the length is seen in the coefficients of variation of the single cultures. The largest coefficient of variation for length is 15.279, while for breadth it is 28.879.

Relation of Length to Nutrition.—In general, increased nutrition increases the length. But the result is not always the same, because increased nutrition has two main effects: to increase directly the size of the adults, and to bring about multiplication. The latter effect, of course, decreases the mean length of the individuals of a culture, since it induces the presence of many specimens that are young, and therefore small. Increase in mean length due to added nutrition is seen in Table XVIII., rows 8 to 9, 10 to 11. *Decrease* in mean length, due to added nutrition is seen in the same table on comparing rows 1 and 2; 3 and 4; 13 and 14; 17 and 18. This decrease is due to the fact that in the nutritive fluid the animals divide before they reach the length of those in the poor fluid.

Decrease of length, due to decrease of nutrition, is seen in Table XVIII., by comparing rows 2 and 6; 7 and 8; 21 and 22; 23 and 24; 23 and 26.

Relation of Breadth to Nutrition.—The relation of breadth to nutrition is simpler than that of length; in all cases increase of nutri-

tion increases the breadth; decrease of nutrition decreases it. The response of breadth to changes in nutrition is immediate and very marked. Within twenty-four hours increased nutrition caused in the *D* line an increase of 49.724 per cent. in breadth (rows 8 and 9, Table XVIII.); in the *c* line it caused in twenty-four hours an increase of 40.778 per cent. (rows 17 and 19, Table XVIII.).

But the decrease of breadth with decrease of nutrition does not vary directly with the time; when plump individuals are left without food, they decrease much more rapidly at first than later. Thus, in the series shown in Table XVIII., rows 2, 3 and 6, the breadth decreased in the first forty-eight hours 21.324 microns, or 32.867 per cent.; in nine days more of lack of food the breadth decreased only 5.476 microns, or 8.440 per cent. more.

Proportion of Breadth to Length.—Since changes in nutritional and other conditions act more readily and more strongly on breadth than on length, and since the same agent may increase the breadth while decreasing the length, the proportion of breadth to length varies greatly under different conditions. The mean index, or ratio of breadth to length, varies in different cultures of the *D* line from 21.337 per cent. to 36.123 per cent.; in the *c* line from 23.067 per cent. to 41.455 per cent. Since the breadth is more dependent on nutritive conditions than is the length, we find the lowest ratio of breadth to length in the starving cultures (rows 8, 26, Table XVIII.); the highest ratio in well-fed cultures (rows 2, 14, 19, Table XVIII.). An increase of nutrition causes uniformly an increase of the ratio of breadth to length; a decrease of nutrition has almost uniformly the reverse effect. A single exception to the relation last mentioned is seen in the change from row 21 to row 22, Table XVIII.; here other causes, connected with conjugation, were probably at work. Whenever the mean breadth increases, the mean ratio of breadth to length likewise increases. (The only exception is the case just mentioned, where conjugation was involved.) It must be understood that this does not mean that in all cases the mean ratio of breadth to length varies directly with the mean breadth; if we compare rows 6 and 7, Table XVIII., for example, we find that this is not the case. But whenever, as a matter of experimental procedure, the mean breadth was caused to increase, the mean ratio of breadth to

length likewise increased. This is due to the two facts mentioned in the first sentence of this paragraph.

Effect of Environment on Variation.—The amount of observed variation, as measured by the coefficient of variation, depends largely on environmental conditions; this is true both for length and for breadth. In the *D* line the coefficient of variation for length varies in different cultures from 6.821 to 13.262;[6] for breadth it varies from 8.896 to 28.879. In the *c* line the coefficient varies for length from 7.134 to 15.279; for breadth from 10.700 to 24.291.

The effects on the coefficient of variation of changes in nutrition vary much in different cases; increased nutrition sometimes increases the coefficient, sometimes decreases it, sometimes produces first one effect, then the other. There are evident physiological reasons for the different effects. In a starving culture the first effect of rich nutrition is to cause many of the individuals to increase in size, while those individuals in which the effects of starvation had gone far do not at first take food and change. Hence there is a great increase in the coefficients of variation; in changing from row 8 to row 9 (Table XVIII.) both coefficients approximately doubled in twenty-four hours. Later, though the animals were kept in the same fluid, the coefficients decreased again—all of the specimens having reached more nearly a condition of equilibrium. If the animals are fairly well fed before the additional nutrition is met, an early effect is to cause rapid multiplication; the consequent presence of both young and old individuals in the culture increases the coefficients of variation, and particularly that for length. An example of this is seen in the change from row 3 to row 4, Table XVIII. A little later, when the multiplication has ceased, the coefficients of variation become small again. The coefficients of variation are likely to be small in starving cultures, owing to the fact that there is little multiplication and the adults have reached a condition of relative equilibrium. By taking into consideration the immediate and the remote effects of a given agent on growth and multiplication, its effects on the coefficients of variation usually become intelligible.

[6] Of course the cultures contain specimens in all stages of growth; as we have previously seen, the coefficient of variation becomes much less when the animals are selected with reference to age.

It is not necessary to emphasize the fact that since different environmental conditions produce different dimensions, the coefficients of observed variation will be much increased by throwing together specimens from different environments, or those taken at different times from the same culture. Examples of this are seen in rows 12, 15 and 20, Table XVIII.

The question may be asked, How can we account for the large coefficients of variation in given lots, taken all from the *same* environment (as in the various "rows" of Table XVIII.)? Surely, it may be said, the age differences among the individuals are not sufficient to account for coefficients of 12, 13, 20, etc., such as we actually find. This is undoubtedly true, and it becomes still more striking when we consider cases like Table XLI. (appendix), where the individuals are all of practically the same age, and all come at one time from the same small watch-glass of hay infusion, yet we find the coefficients of variation to be respectively 6.389 and 14.615. The considerable variation is to be understood only by realizing that even a small mass of fluid constitutes a relatively large and varied environment for *Paramecium*. A watch-glass of hay infusion is a microcosm to this animal. Bacteria gather on the surface, while they may not be found on the bottom or through the middle. The bacterial zoöglœa may become thicker at one edge than at the other, owing to the accidents of the original distribution of the seed bacteria or of the infusoria. Some of the *Paramecia* thus get more food than the others, perhaps at a critical period of growth; they thus get a start, which enables them perhaps to obtain more food than the others, even under uniform conditions. Some of the individuals get crowded away from the bacterial zoöglœa, and remain against a rough spot on the glass instead, where they get no food. In short, even in a few drops of water the conditions are *not* uniform throughout; some of the animals are well nourished, others poorly nourished, and the results show in the variations of their measurements.

The question whether some of the variations in such cases are not congenital and hereditary will be taken up later; we shall find little evidence that this is the case.

It is clear that no particular coefficient of variation can be considered characteristic of a particular race, except as the conditions

are very precisely defined. If all conditions of environment and growth were made absolutely the same, there is reason to believe (as we shall see farther) that for a given line (descended from a single individual) the coefficient of variation would be very close to zero. Its actually observed value in a given lot then depends almost entirely on environmental and growth differences.

Effect of Environment on Correlation.—The observed correlation between length and breadth varies greatly under different environmental conditions. In the *D* line the coefficient which measures correlation varies in different cultures from .3906 to .8463; in the *c* line from .4141 to .8500 (see Table XVIII.). Such differences are easily and quickly produced by environmental changes; thus the two extremes just mentioned for the *D* race were found in samples of the same lot of *Paramecia* taken twenty-four hours apart—one before, the other after, the addition of a nutritive fluid.

The correlation between length and breadth expresses the accuracy with which length and breadth vary proportionately. The actual proportion of one to the other, in a given lot, is, of course, of no consequence; length and breadth might be the same, or one might be 50 per cent. or 1 per cent. of the other; the correlation would still be complete (1.000) provided this same proportion were maintained throughout the particular lot examined. Any factor which causes the proportion of breadth to length to vary in a given lot, of course causes the correlation to fall below 1.000. If in a given lot many different ratios of breadth to length are represented, the correlation is, of course, lowered. In such a lot, any factor which tends to make the proportion of breadth to length more constant, of course, increases the correlation.

Examining the various factors which have the effects just mentioned, we find that the observed correlation depends upon many things.

(*a*) In considering the effects of growth (page 455), we saw that the proportion of breadth to length differs in different stages. Some of the effects of the environment on correlation are due to its effect on multiplication and growth.

(*b*) Certain environmental agents (as increased nutrition) increase the breadth while decreasing the length. Now, if this happens at

the same time and in the same proportion in all the individuals, then at any given moment the coefficient of correlation will, of course, not be altered by it. But if for any reason the changes occur more quickly or strongly in certain individuals than in others (as is usually the case), then, of course, the coefficient of correlation will be decreased. Or, if we throw together individuals taken at different stages of the process, the correlation becomes greatly decreased; it may even become negative. For examples, see rows 15 and 20, Table XVIII.

(*c*) Even if a given agent causes a change in the same direction (*e. g.*, an increase) in both length and breadth, the inclusion of different stages in the process may reduce the correlation (if it is already high). This will occur (1) if the two dimensions are not changed proportionately to each other, and (2) if the change in a given dimension varies at different stages of the process. Both these conditions, as we have seen, are fulfilled in the changes in dimensions induced by the environment. Under almost any environmental change breadth is altered more than the length. Furthermore, when nutrition is decreased, breadth decreases more rapidly at first than later. The inclusion of different stages of the process in a collection therefore results in the inclusion of various different proportions of breadth to length—lowering the correlation.

(*d*) If the correlation is already low, indicating the presence of many different ratios of length to breadth, then varied changes in these ratios may compensate some of the existing differences, causing an increase in the correlation. Whether this shall or shall not occur depends upon the condition of affairs before the changes are made, and on the nature of the changes themselves. A special case of this comes up in the next.

(*e*) When a culture containing thin, poorly fed individuals is given added nutriment, the correlation between length and breadth increases (compare, in Table XVIII., rows 1 and 2; 8 and 9; 10 and 11; 13 and 14; 17 and 18; 17 and 19, etc.). This is because, when fresh nutriment is added, the thinnest, poorest-fed individuals naturally take more food than do the individuals that are already plump and well-fed; they therefore increase most in breadth. As a result, existing differences in breadth are compensated; all the animals take

on that relative proportion of breadth to length that belongs to well-fed specimens.

Thus, we find almost throughout that an increase in the ratio of breadth to length is accompanied by an increase in the coefficient of correlation; a decrease in the ratio of breadth to length by a decrease in the coefficient of correlation. Examining these two constants, in the last two columns of Table XVIII., we find this relation to hold in every case of experimental procedure save one. (In the change from row 3 to row 4 it does not hold; this is due to another factor, to be taken up later.) If without regard to experimental procedure, we merely compare the mean index (or ratio of breadth to length) with the coefficient of correlation, we find the relation a little less general, though still marked; a large mean index is usually accompanied by a high coefficient of correlation.

Since, as we have previously seen, greater breadth is usually accompanied by a higher mean index, it follows that greater breadth is likewise usually accompanied by a higher correlation between breadth and length. This is, on the whole, evident on inspection of Table XVIII., though since other factors are involved, the relation is not without exception. But in general, broader specimens tend to show a more constant proportion of breadth to length than do thin ones.

(*f*) In poorly-fed cultures, as we have just seen, the breadth is apt to be variable in proportion to the length (giving low correlation) because some of the individuals get more food than others. But if all are reduced to an actually starving condition, then this source of variation is removed, and we may again get high correlation between breadth and length. This condition appears to be realized in row 26 of Table XVIII. Here a large culture had been reduced by starvation to a population of but 37, and these give the very high correlation of $.8018 \pm .0396$.

(*g*) When a given agent causes rapid multiplication, so that the sample taken includes many different stages of growth, with their different proportions of breadth to length, the correlation becomes low. This is the reason for the marked decrease in correlation in changing from row 3 to row 4 in Table XVIII.

All together, it is clear that no particular coefficient of correlation

can be taken as characteristic of a particular race of *Paramecia;* certainly not without very precise definition of the conditions. It appears probable that if all conditions of environment, growth, food taken, etc., could be made absolutely the same for individuals derived from the same ancestor, the coefficient of correlation would be close to 1.000.[68a] By varying these conditions any degree of positive correlation, down to zero, and many degrees of negative correlation can be attained.

V. INHERITANCE OF SIZE.

Having examined the effects of growth and of environment on size and form, we are now prepared to investigate how far these are determined by internal factors, handed on from parent to progeny. Without such a preliminary study of growth and environmental action it would be impossible to investigate successfully the heredity of size and form.

We have already seen that not all differences in size are due to growth and environment; in the first culture examined (Table I., page 398) there were at least two sets of individuals of characteristic different sizes, and these differences in size are lasting. Progeny of the two typical individuals *D* and *c,* from these two sets, still retain their characteristic relative sizes after more than a year of culture under all sorts of conditions.

The differences between these two sets are about the same as those which have been described as distinguishing two species, *D* corresponding to the accounts of *Paramecium caudatum, c* to *Paramecium aurelia.* The next problem is to determine whether there are still other races of *Paramecium,* distinguishable on the basis of differences in size, independently of the environment. Can we by selecting individuals of differing sizes isolate races of corresponding sizes? Can we find races of all sorts of sizes intermediate between the largest and smallest adult representatives of such a heterogeneous culture as is shown in Table I.?

The clear grouping of the culture of Table I. into two sets seems to indicate that we have present simply two races or species. My

[68a] Of course if all variation disappeared, as would perhaps be the case, then the concept of correlation would have no further application.

first experiments consisted of attempts to break the two lines derived respectively from *D* and *c* into other races of different sizes by selection and breeding of individuals of different sizes. This led incidentally, as we have seen, to the study of the effects of growth and environment on size; it was found that the observable differences between different members of either race were due to these factors, so that selection of such members did not lead to the establishment of races of different sizes. The results of a large amount of time-consuming work along this line, done before the investigation of growth and environmental action, were throughout negative.[7]

As a result of this work, I was disposed toward the belief that the characteristic sizes of *D* and *c* represent conditions of stability, which have properly been distinguished as two species, and that races of other sizes were not to be found or produced.

But the work thus far has, of course, been based on "pure lines," in the sense in which that expression is used by Johannsen (1903, 1906). The lines *D* and *c* are each derived from a single individual, reproducing asexually, so that no admixture from outside has entered them during the experiments. Now, while it appears difficult or impossible to produce other races *within* these pure lines, there remains, of course, the possibility that still other lines exist in nature. Can we find in a "wild" culture, by proper selection of differing individuals, still other races of differing size? This was the question next investigated.

1. Selection for Different Races in a Wild Culture.

(*a*) *Races Isolated from Cultures Not Conjugating.*

Attempts to separate out other races than those represented by *D* ("*caudatum* form") and *c* ("*aurelia* form") were first made with a wild culture which I called *OI*. This culture developed in decaying vegetation from a marsh. It contained two well marked sets of individuals: (1) very large individuals, corresponding in many respects to the *D* line, but with a mean length on January 3, 1908, of 238.280 microns; these we will designate *E*; (2) smaller

[7] To the experiments on selection within a pure line we return in a later section.

individuals corresponding in many respects to the *c* line, with a mean size on November 14, 1907, of 140.133 microns. These two sets occurred mixed, but each reached its maximum development at the dates mentioned. Isolated samples of the two sets retained their characteristic differences in size, just as happened in the case of *D* and *c*.

But the interesting condition showed itself in the smaller set. Among these were individuals of such different sizes, that in spite of our knowledge of the great differences produced by growth and environment, it seemed worth while to try to isolate and breed them. In a random sample of 60 specimens the length varied from 96 to 176 microns—the smaller sizes being grouped about 120 microns, the larger about 160 microns.

Accordingly, on November 9, 1907, I separated two lots, one containing ten of the smaller specimens, the other ten of the larger ones. These were placed in watch-glasses with equal quantities of the same culture fluid, and kept under identical conditions, where they were allowed to multiply. One week later (November 16) thirty specimens measured from each showed mean dimensions of 125.600 × 36.200 microns for the progeny of the larger ten, 96.400 × 30.00 microns for the progeny of the smaller ten. On November 27, a random sample of 100 from each gave for the progeny of the larger ten, dimensions of 134.320 × 36.280 microns; for the smaller set, 92.240 × 26.920 microns. Thirty-seven days later (January 2, 1908) the two lots still showed their characteristic differences, though cultivated under identical conditions. The mean dimensions of the two sets (from random samples of 100) were now 134.360 × 33.440 microns (for the larger), and 104.208 × 26.583 microns (for the smaller).

Thus, we have clearly two sets, with differences in size persisting from generation to generation (in spite of fluctuations in each due to environmental changes), and both falling, in a general way, in the dimensions previously found for the line *c*. It is evident, therefore, that *D* and *c* did not represent the only existing different lines.

Since the two sets under experimentation had come each from ten individuals which may be of heterogeneous origin, I isolated from each, as soon as it was evident that they were retaining their

differences, a single characteristic individual. This was done on November 13. The specimen from the larget set I called *g*; it measured approximately 130 to 140 microns in length. The specimen from the smaller set I called *i*; its length was about 90 to 95 microns. These two individuals were kept under the same conditions and allowed to multiply.

The small specimen *i* multiplied more rapidly than the large one *g*. On November 16 there were but seven progeny of *g*, while *i* had produced a large number. Two typical specimens of *g* were killed and gave measurements of 160×48 microns and 164×56 microns. Five typical specimens of *i* ranged in size from 92×36 to 128×44 microns, with a mean of 103.2×39.2.

Evidently, therefore, the progeny of *g* and *i* tend to retain the differences in size characteristic of the parents. The two lines were kept for a long time, under the same conditions; at intervals random samples were measured. The measurements at different dates, with the number of specimens on which they are based are given in Table XXIII., p. 488. (The small numbers of specimens employed on certain dates are due to the fact that only a small number existed at that time.)

The great fluctuations in the dimensions of each line will of course surprise no one who has examined that part of this paper which deals with the effects of the environment. These fluctuations are due mainly to differences in nutritional conditions. At intervals it was necessary to add new culture fluid; the dimensions in both lines thereupon rose at once; they then gradually declined till new fluid was added. Details on this matter are not necessary for our present purpose.

The important fact is, that in spite of all fluctuations, the lines *g* and *i* retained throughout the three months in which they were under observation their characteristic relative sizes. Multiplication was probably at the rate of about one fission a day, so that the table represents 90 to 100 generations. We have here two lasting races comparable to the two races from our first culture, which we called *D* and *c*. It is clear that neither *g* nor *i* is identical with *D*, since the latter is much larger; whether either is the same as *c* we shall inquire later.

TABLE XXIII.

Comparative Sizes in Microns of g and i and their Progeny at Different Dates, when Cultivated under the Same Conditions.

Date.	*g* and Its Progeny			*i* and Its Progeny.		
	No. of Specimens.	Mean Length.	Mean Breadth.	No. of Specimens.	Mean Length.	Mean Breadth.
1907						
Nov. 13	1	130–140	35–40?	1	90–95	30–40?
" 16	2	162.000	52.000	5	103.200	39.200
" 18	7	140.000	40.000	12	103.666	35.666
" 23	30	129.333	34.933	30	88.268	30.268
" 26	100	137.120	38.720	100	99.560	28.200
Dec. 7	61	120.590	41.110	96	98.709	34.208
" 16	17	127.059	38.588	23	98.608	29.739
" 30	40	112.600	31.300	64	86.756	22.062
1908						
Jan. 2	100	146.640	40.600	100	106.680	26.400
Feb. 5	57	116.912	36.070	43	93.583	27.500

It will be recalled that in the original culture from which came *g* and *i*, there was a still larger set which we called *E*. Ten of these were selected and cultivated under the same conditions as *g* and *i*. They retained throughout their much larger size (numerical results are given later), so that from this culture we have isolated three lines or races which retain their differences in size under the same external conditions.

At this period, then (January 1, 1908), I had in the laboratory a number of lines or races which had been studied with care. These formed two sets, so far as our knowledge of them up to this point is concerned. The two lines, *D* and *c*, from culture *I*, were clearly distinct even under identical conditions. The three lines, *g*, *i* and *E*, from the second wild culture *OI*, are likewise clearly distinct from each other. But the relation of *g*, *i* and *E* to *D* and *c* is uncertain; we may have on hand five distinct lines, or only four, or three.

To determine whether any of these five lines are identical, it is necessary to cultivate all five under the same conditions. A certain number must be selected from each; these must be brought into the same culture fluid and allowed to multiply in the same environment.

It is extraordinary what difficulties are presented in carrying out this apparently simple plan. The different lines have become adapted to certain diverse nutritive conditions; if now they are brought at once into the same culture fluid, some of them die. In the present case, *g* and *i* had been living in comparatively fresh hay infusion, *D* and *c* in different old hay cultures, *E* in a culture of decaying pond weeds. When all were brought into fresh

hay infusion, *E* died at once, *c* after a day or two; *D* multiplied slowly, then died in the course of a week or so, while *g* and *i* throve and multiplied.

It was therefore necessary to bring the different lines gradually into the new fluid, by mixing some of it with the fluid in which they lived, increasing the proportion of new fluid at intervals. This was found to be a very delicate undertaking. Certain of the lines would thrive for a time, under this procedure, then would begin to degenerate; in this way much time was lost. Finally, however, the different sets were induced to thrive in the same hay infusion.

Procedure Necessary for Making the Conditions Identical for Different Lines.—The procedure followed, in order to be certain that the cultural conditions were the same for all, was as follows: From each race ten typical individuals were selected. These were mixed with gradually increasing amounts of hay infusion, in the way just set forth—while at the same time of course they multiplied in number. After they had all gotten accustomed to the infusion, it was necessary to take measures to assure the identity of the solutions in which the different sets were living. For this it is not sufficient merely to transport the individuals to definite quantities of the same nutritive solution. For up to this point each set has been living in a solution which has received an admixture of the original culture for that set. Now, *these different original cultures contained different kinds of bacteria.* On transferring the infusoria to the hay infusion, they of course carried some of their own bacteria. By repeated changes the number of bacteria introduced could be much reduced. Nevertheless different kinds were brought in in different cases, so that we still have the different lines in cultures of diverse bacteria. From this fact naturally diverse chemical properties may develop in the different cultures, though the basic nutritive solution is the same. These diverse chemical properties would of course modify the organisms, making it impossible to compare them with regard to inherited size. To make the conditions of existence the same, *it is not sufficient to attend merely to the basic fluid; the bacteria in the fluid must also be the same.* This is a principle of wide practical importance in all experimental work with such infusoria. It is not a mere theoretical requirement; death frequently results from the introduction of a certain kind of bacteria into a certain culture, while another culture of identically the same fluid flourishes, because the bacterial infection is different.

This requirement was met in the following way: After the different sets had become acclimatized to the same hay infusion, ten of each were removed with a fine capillary pipette, and washed twice in fresh hay infusion. The second washing of the different sets was done *in the same mass of fluid,*—a small watch-glass full. The different sets might of course each carry with them a few of the bacteria characteristic of their original culture. After all had been washed in the same mass of fluid, this fluid would of course be infected with bacteria from all the different sets. Now, after the washing was finished, a definite quantity of this fluid in which all had been washed *was added to the final culture fluid for each lot.*

Thus each lot of ten is in the same quantity of the same nutritive fluid,

and infected with the same bacteria as all the others. All are kept in watch-glasses of the same form and size, close together in the same moist chamber. Any characteristic differences in the resulting progeny must then be due to conditions within the animal, and not to differences in the environment. If we reach the same result, not merely in one experiment, but in a series conducted in this manner, we can be sure of our results.

Cultures of the five lines, *D, c, g, i* and *E,* prepared in the way just described, were set in progress January 19, 1908. In order to determine with certainty how much effect possible environmental differences might have on the results (as well as for certain other purposes), two lots each of *D, g* and *i* were used. If the two lots of *g,* for example, show differences as great as those between *g* and *c,* then, of course, we have no ground for considering *g* and *c* inherently different; the environmental differences account for all. These lots were allowed to multiply till February 5. Then a sample of each was killed and measured. Now a new lot of ten of each set was prepared by the methods given above, and the animals were again allowed to multiply till February 15, when samples were again measured.

It will be recalled that *E* is a lot derived from ten specimens of possibly diverse ancestry, from the culture *OI,* with an original mean length of 238.280 microns; that the line *D* has shown in repeated determinations a highest mean length of 202.280 microns (Table XVIII.); that *c, g* and *i* are smaller lines, derived from single individuals; *g* is known to be larger than *i,* but the relation of *c* to these is unknown.

The results of these breeding experiments are given in the following Table XXIV.

The experimental results given in this table show certain things clearly.

1. The method of culture is adequate for bringing out the inherent differences in different lines without confusion due to environmental effects. This is shown by the fact that when two cultures are made from certain single lines, these show themselves after breeding for many generations to be nearly identical, while the different lines give diverse results. In only one case (*D* on February 15) is there a notable difference btween the two samples of a single line, but this is much less than the difference between that line and any other.

TABLE XXIV.

Mean Dimensions in Microns of the Five Lines E, D, c. g and i, when Cultivated under the same Conditions, January 19 to February 5 and February 5 to February 15.

Date.	Dimensions of *E*.		Dimensions of *D*.		Dimensions of *c*.	
	Number Measured.		Number Measured.		Number Measured.	
Feb. 5	43	169.395×52.930	57	(1) 169.754×46.877	60	99.667×26.333
			19	(2) 169.895×43.579		
Feb. 15	100	200.320×52.400	100	(1) 180.240×46.880	100	100.320×26.480
			100	(2) 173.240×49.760		
Feb. 27	100	172.040×55.520	100	175.360×47.160		

Date.	Dimensions of *g*.		Dimensions of *i*.	
	Number Measured.		Number Measured.	
Feb. 5	50	(1) 114.720×33.920	50	(1) 92.000×26.960
	57	(2) 116.912×36.070	48	(2) 93.583×27.500
Feb. 15	100	125.240×35.440	100	95.440×30.040

2. At least four distinct lines are present, *D*, *c*, *g* and *i*; these maintain their relative different sizes throughout the experiments, which lasted about twenty-five generations.

3. The lines *E* and *D* are nearly or quite the same. On February 5 they show nearly the same measurements, but on February 15 there was a marked difference. To test the meaning of this these two were cultivated twelve days more; then on February 27 they gave again nearly the same measurements. It will doubtless be safest to consider them the same.

We have now, therefore, four different lines or races of *Paramecium*, characterized by persisting relative differences in size. One of these (*D* and *E*) belongs, from its size, to the "*caudatum* group"; the other three are much smaller and fall in the "*aurelia* group." Of these, *g* is the largest, *i* the smallest, while *c* is intermediate. Under a similar change in the environment these all change in a corresponding way, as is shown by the fact that on February 15 all were somewhat larger than on February 5. It may be noted that

the differences in size among these four lines were very evident to the eye on inspection with the low power of the microscope, and that the difference was clearly present at all periods between the dates when the measurements were made. The measurements merely make precise what is evident to the eye without them.

Before attempting to determine whether still other lines can be isolated, and particularly whether it is possible to fill the wide gap between the *caudatum* group and the *aurelia* group, another question must be investigated—a question which strikes at the foundation of our conclusions up to this point. This is the question of the relation of these lines of diverse size to conjugation and the life cycle.

(*b*) *Are the Lines of Different Size Merely Different Stages in the Life Cycle?*

Calkins (1906) and others have set forth the fact that *Paramecium* and other infusoria show different dimensions in different stages of the life cycle—the cycle which begins with conjugation, extends over many generations of reproduction by fission, and ends with another conjugation. The question arises, therefore, whether our lines of diverse dimensions are not merely different stages in the life cycle; whether they would not, if brought to the *same* stage of the cycle, show the same dimensions. This possibility must be investigated before we proceed farther.

The details of the relation of conjugation and the life cycle to variation, inheritance, etc., are to be dealt with in a separate paper of this series. But since the question which stands at the head of this section is an absolutely fundamental one for the proper interpretation of the results of the present paper, it must be dealt with here.

To answer this question, it is evidently necessary to proceed as follows: Cultures showing epidemics of conjugation must be examined for conjugating pairs of diverse sizes. If such are found, the individuals must be isolated and allowed to multiply, in order to determine whether the progeny retain the diverse sizes characteristic of the parents. If from a conjugating culture we can obtain diverse lines standing all in the same relation to conjugation and the life cycle, then evidently our diverse lines represent something more

than different stages in the life cycle. The problem also can be attacked in certain other ways, which will be described.

The relation of diverse sizes to conjugation and the life cycle was studied with special thoroughness in the case of a culture in which there was an epidemic of conjugation January 29, 1908. This culture was found in decaying vegetation from a small pond near Baltimore; I called it culture *M*. Table LXI. (appendix) shows a random sample of this culture, including both conjugants and non-conjugants; of the 238 specimens in the table, 38 were conjugants, 200 non-conjugants.

From this culture *M* a large number of pairs were isolated, for various purposes, and allowed to multiply. Without going here into the details of the experiments, on February 21 I had from this culture eight sets or lines, each descended from a single equal pair or a single ex-conjugant; these lines were designated in my notes *L2*, *G1*, *A1*, *A2*, *I*, *C2*, *F1* and *F2*. (The designations are the same as those given to the original pair or individual from which the lines came.) In addition to these eight "pure lines," I had two cultures derived each from eight pairs of conjugants of approximately the same size; these were called *K1* and *K2*. A final culture was derived from ten small, nearly equal, non-conjugants from the same culture; it was designated *H*.

It is, of course, unfortunate that it is not possible to measure accurately the original living individuals from which the different lines are derived, but this will not alter in any way the results on the problem in which we are at present interested. The essential question is whether the lines derived from the different pairs or individuals are identical or diverse in size.

These various cultures were kept, so far as possible, in the same nutritive fluid and under the same conditions. Marked differences in size were apparent on examining the different sets with low power of the microscope. On February 21 fifty individuals of each of these eleven different sets were brought, with all the precautions mentioned on page 489, into the same culture fluid, while at the same time fifty specimens each of *D* and *g* of our earlier pure lines (see page 491) were brought into the same fluid. These were all allowed to multiply till February 26, when a random sample of 100 or more

of each was killed and measured. Later, on March 7, twenty individuals were taken anew from each of these thirteen lots, brought again with elaborate precautions into the same culture fluid, kept under the same conditions and allowed to multiply, part till March 13, part till March 19, when other samples were killed and measured. From our previous extensive experience with *i* and *g* (Table XXIII., page 488) and with five lines of Tables XXIV. (page 491), we can be assured that two sets of measurements taken at such intervals will give us reliable data as to the existence of any considerable lasting differences among the different lines. The results of the measurements of the thirteen different sets are given in classified form in Table XXV.

TABLE XXV.

Mean Dimensions in Microns, of the Thirteen Sets Described in the Text, after Cultivation under the Same Conditions, February 21 to February 26, and March 7 to March 13 (or March 19). (The conditions before; and in intervening periods were essentially the same, but elaborate precautions were taken for the periods specified). All are from the conjugating culture *M*, of January 29, save the last two sets.

Line.	Number Measured.	February 26.	Number Measured.	March 13.	Number Measured.	March 19.
		(1) Descendants of Pairs.				
L 2	100	206.360 × 60.840	100	220.560 × 59.960		
G 1	100	201.400 × 52.400	100	210.960 × 52.200		
A 1	100	193.560 × 51.840	100	203.640 × 52.560		
A 2	100	184.640 × 50.760	100	187.878 × 44.490		
I	100	132.880 × 41.960			100	138.880 × 43.120
C 2	100	128.880 × 40.400			100	119.200 × 37.280
		(2) Descendants of Single Ex-conjugants.				
F 1	100	193.000 × 50.840	56	209.643 × 56.643		
F 2	100	182.200 × 51.040	100	199.960 × 50.120		
		(3) Descended each from 8 Equal Pairs.				
K 1	100	133.680 × 39.400				
K 2	100	125.920 × 37.040			100	125.000 × 42.520
		(4) Descended from 10 Small Non-conjugants.				
H	100	131.400 × 42.000			100	128.840 × 41.360
		(5) Older Lines, not from Culture *M*.				
D	111	176.901 × 50.018	120	187.033 × 49.100		
g	100	124.440 × 35.920				140.800 × 39.640

Examination of this table shows that lines derived from different conjugating pairs or different ex-conjugants do differ from each other at the same periods in the life cycle, even though living under

identical conditions. The differences are fully as marked as those found among diverse lines derived from individuals not conjugating and taken without reference to the period in the life cycle in which they happen to be.

Besides this general result on our main problem, the following important facts are brought out by the table:

1. The six lines derived from the six different pairs (first six of the table) are clearly distinct. They show parallel differences in both sets of tests; the order of dimensions from largest to smallest is the same in both the first and the second measurements, though these are separated by at least fifteen generations.

2. The two lines, *F1* and *F2*, derived from single ex-conjugants, are likewise distinct from each other. So far as the measurements go, *F1* may possibly be the same as *A1*, *F2* as *A2*.

3. Certain different sets are likewise found in the other lots of the table.

4. The different sets fall into two very distinct groups, whose dimensions are separated by a wide interval. To the large group belong *L2*, *G1*, *A1*, *A2*, *F1*, *F2* and *D*. To the small group belong the others. The greatest mean length of any set of the smaller group (140.800 microns) differs widely from the least mean length of any set of the larger group (176.901 microns). These two groups correspond in general to what we have heretofore called the "*aurelia* form" and the "*caudatum* form."

As there was no danger of confusing any lot of the larger group with any lot of the smaller one, the second measurements of the two groups were not made for the same day; the lots of the larger group were killed March 13, while those of the smaller group were not killed till March 19, as the table shows. This was done on acount of the great labor involved in selecting, with capillary pipette, killing properly, and preserving, so many different sets on the same day. This difference of treatment of course does not alter the comparability of the different sets within a given group, which is all that we require.

5. How shall we decide which of the thirteen different sets form distinct lines? For this it will be best to take into consideration mainly the length, since we know from our earlier studies that little significance is to be attached to difference in breadth, owing to the extreme changes in that dimension with slight differences in food.

If any two sets differ in length in the same way at both measurements (taken many generations apart) and if the differences between them are each time decidedly greater than the sum of the probable errors of the measurements of the two, then we can be assured that we are dealing with really differentiated sets. Now, examination of the extensive series of measurements in Tables X. and XVIII. shows that the probable error of the mean length never reaches two microns, even when the number of specimens is much smaller than in our present measurements, and when conditions are of the most varied character. It is practically certain that the probable error of the mean length would not amount to one micron in any of the comparatively homogeneous sets with which we are here dealing. If, then, we require a difference of four microns between the mean lengths of the two sets, this difference to have the same sign (+ or —) at both measurements, we shall be within safe limits. Applying this test, we find four lines clearly distinct in the larger or "*caudatum*" group, while in the smaller or "*aurelia*" group we can be certain of but two distinct lines (represented best perhaps by *I* and *C2*). We have previously found three distinct lines in the *aurelia* group (*c*, *g* and *i*, Table XXIV.), so that all together we now have at least seven different lines of *Paramecium*, showing constant relative differences in length. It is probable that very exact tests would show the distinctness of some other lines of Table XXV.

The striking difference between adults of different races, under varied conditions, is shown in Fig. 7. Here we have two adults, one belonging to our smallest race (*i*); the other to one of the large races.

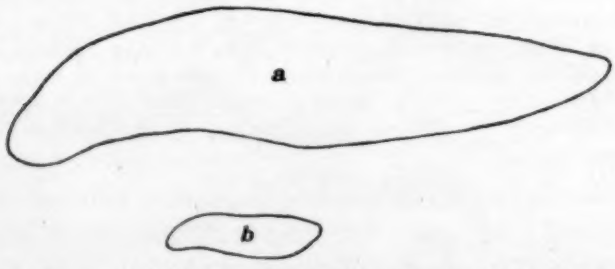

FIG. 7. Extreme adult sizes from different pure lines of *Paramecium*. *a*, large individual from a large line. *b*, small individual from the small line *i* of Table XXIII., page 488. Both magnified 235 diameters.

It is clear, then, that the question placed at the head of the present section is to be answered in the negative. The diverse lines of different size are *not* merely different stages in the life cycle.

(*c*) *Other Evidences of Permanent Differentiation in Size, Independent of the Life Cycle.*

The proof just given, that lines beginning with conjugants are differentiated in size even in the same portion of the life cycle and under the same conditions, is conclusive. But it may be worth while to give briefly certain other evidences of the same thing.

1. First we have the fact that in a given culture the conjugants themselves differ in size; this has already been shown by Pearl (1907). In a certain Culture IV., I found conjugants varying in dimensions from 148×44 to 260×60 microns. I have found (not in the same culture) conjugants with length as low as 100 microns. It is clear, therefore, that not all individuals are of the same size at conjugation. There is no reason to expect them to be so, therefore, at other definite periods in the life cycle; as we have seen, they are not. Selection of small pairs gives small progeny; of large pairs, large progeny.

2. In certain of my pure lines whose history was followed for a long time and whose dimensions were taken at intervals, conjugation occurred at times, but the dimensions at such times were not very different from the dimensions at other periods in the life history. Thus, in the earlier sections of this paper we have dealt with two pure lines, *D* and *c;* the former showed usually a mean length of about 180 microns, the latter a mean length of about 130 microns (see Table XVIII.). At a certain time an epidemic of conjugation arose in *c*. The mean dimensions were indeed higher than usual at that time, the mean length of the conjugants rising to 158.496 microns. But this does not by any means bring it up to the ordinary mean of *D*, and immediately after conjugation (in five days) the mean length of *c* fell back to 129.640 microns. Again, in the small race *g*, of Table XXIII., conjugation occurred in a number of cases; a typical pair measured but 110 microns in length. In other lines I have found for the conjugants means as high as 199.024 and as low

as 116.856, and these were correlated with corresponding measurements throughout the series.

These facts, of course, do not show that the size may not change at the time of conjugation or before or after. What they do show is that any differences thus produced do not account for the permanent differentiations we have found among different lines. We may distinguish (1) differences in size due to growth; (2) those due to nutrition and other environmental conditions; (3) those due to different stages in the life cycle (as a rule not marked in comparison with the others); (4) inherent, hereditary differences in size, persisting when all other conditions are made the same.

(*d*) *Lines Intermediate Between the Two Main Groups. The Question of Species in Paramecium.*

As we have already noted, the seven differentiated lines which we have thus far distinguished fall into two main groups, separated by a wide interval. In Table XXV. we find one group with mean lengths varying from 119.200 to 140.800 microns, while in the other group the mean lengths vary from 176.901 to 220.560 microns. Between the two there is thus a gap of 36.101 microns in which none are found. Is this gap constant and characteristic, so that our two large groups are permanently differentiated? If so, we should have some real basis for the common distinction into two species, *Paramecium caudatum* (larger) and *Paramecium aurelia* (smaller). The fact that we find in nature such cultures as that shown in Table I. (page 398), in which the individuals are distinctly separated into the two groups, seems to raise a presumption that the groups are natural ones, not due to accidents of selection.

For a long time I found no pure lines that were intermediate between these groups. It is possible that this was partly due to a tendency to choose for breeding the largest and smallest specimens, rather than intermediate ones, since my purpose at first was to determine whether there were any permanent differentiations at all; for this, marked differences were desirable.

In the course of work on certain problems connected with conjugation, I came in possession of a pure line, *Nf2*, descended from a single ex-conjugant. This, when cultivated in the usual hay infu-

sion, gave, under various different conditions, the following mean lengths in microns (each mean is based on measurements of 100 individuals): 148.197, 151.920, 158.760, 153.320, 160.852, 156.482.

It is evident that these means fall in the gap separating the "*caudatum*" group from the "*aurelia*" group. I therefore decided to cultivate these under identical conditions with a typical representative of each of the two main groups. For this purpose I chose *D* and *c*, the two lines longest cultivated, which I had used for the study of growth, environmental action, etc. (Tables X., XVIII., etc.). Twenty-five specimens, each of the three lines, *D*, *c* and *Nf2*, were brought on May 1, with the precautions described on page 489, into the same quantity of the same hay infusion and allowed to multiply till May 5. On that date a random sample of each was killed. Though the samples were large, extrinsic conditions prevented my measuring more than the numbers mentioned below; larger numbers would not have altered the results by more than one or two microns in any case. The mean dimensions of these three lines, cultivated under identical conditions, were

D (31 specimens), 202.710 × 51.871 microns.
Nf2 (33 specimens), 168.970 × 48.970 microns.
c (43 specimens), 126.605 × 44.930 microns.

Thus, the dimensions of *Nf2* lie almost precisely half way between those of *D* and *c* (the dimensions exactly half way between would be 164.658 × 48.401). We have, therefore, in *Nf2* an eighth pure line, intermediate between the "*caudatum*" and "*aurelia*" groups formed by the other seven. These two groups are then not separated by an unbridged gap.

The other character which had been held to separate *Paramecium caudatum* from *Paramecium aurelia* was the presence of but a single micronucleus in the former, while the latter had two. Calkins (1906) showed that in the same pure line we sometimes have two micronuclei, sometimes but one, so that this is not sufficient ground for distinguishing two species. Though the present study has shown that differences in size among different lines are more permanent than the data available to Calkins had seemed to indicate, this does not give any better basis for distinguishing two species, since we

have been able to isolate, not merely two permanently differentiated lines, but eight. Of course, it would require merely more extensive and intensive work to isolate others; doubtless the number to be isolated would depend only on the accuracy of the methods used.

To my great regret, I was unable to take the steps necessary to determine the number of micronuclei in the various pure lines with which I worked. The animals multiply so rapidly that with several lines in progress it is quite impossible even to keep up with the data for size alone; probably half my experiments were lost on this account, after much work had been spent on them. It was then out of the question to carry on at the same time the staining processes necessary to determine with certainty the number of micronuclei. For work of the kind presented in this paper, a syndicate of investigators is needed for keeping track of the various important aspects of the matter. In the case of two of my lines the number of micronuclei was determined; *D* (larger) had one; *c* (smaller) had two.

I may be permitted to add to the precise data thus far given a personal impression or surmise. Though, as I have shown, intermediate lines occur, I believe it will be found that most *Paramecia* can be placed in one of the two groups that we have called "*caudatum*" and "*aurelia*." In other words, if my impression is correct, most lines will have a mean length either below 145 microns or above 170 microns; rarely will lines be found whose mean falls between these values. Such at least has been my experience in a large amount of work. Furthermore, I am inclined to believe that those belonging to the smaller group (mean length below 145 microns) will be found to have as a rule two micronuclei; those belonging to the large group but one micronucleus. This matter is worthy of special examination.

(*e*) *Do the Diverse Lines Differ in Other Respects Besides Dimensions?*

In the investigations above set forth the dimensions, and especially length, were made the basis of study, simply because they were the characters most readily examined. Most other characteristics are not easily handled in so minute and relatively undifferentiated an animal as *Paramecium*. But there is, of course, no reason to

suppose that the relations we have brought out are limited to length alone. Probably other differentiated pure lines could be distinguished on the basis of other characteristics.

The only other characteristic on which our data might give results is that of *form*, as distinguished from size. Are some races broader, some narrower, in proportion to the length?

We may first examine this question with reference to the two main groups into which most of our lines fall. Is there any general difference in the proportion of breadth to length when we compare the larger races ("*caudatum* group") with the smaller ones ("*aurelia* group")? The experiments whose results are summarized in Table XXV., page 494, give us data for a number of different lines of both groups, cultivated under the same conditions. We may, therefore, determine the proportion of breadth to length in these. The more accurate way of doing this would be by means of the formula given on page 399. This, however, would involve much computation not made for other purposes; and we may reach very nearly the same results by simply dividing the mean breadth by the mean length. If the differences between the different races are not sufficient to show clearly under this treatment, they are doubtful and inconsequential. The following table gives the ratio of mean breadth to mean length in the different lines represented in Table XXV.; the lines are arranged according to relative size, so as to exhibit any differences between the large and small groups.

The table shows that the ratio of breadth to length is almost uniformly greater in the small or *aurelia* group than in the larger. The lowest ratios of the *aurelia* group are, indeed, a little below the highest of the *caudatum* group, but the difference between the groups as a whole is unmistakable. The first column of the table is the most satisfactory in this respect, since both sets were killed at the same time. In the second column the difference between the ratios for the two groups is still more decided, but environmental differences may play some part in this case. The average ratio for the *caudatum* group is, from the first column 27.473 per cent.; from the second 25.679 per cent. For the *aurelia* group the averages are: first column 30.441 per cent.; second column 31.319 per cent. The

TABLE XXVI.

Ratio of Mean Breadth to Mean Length in the Lines and Races of Table XXV., page 494, Cultivated under Identical Conditions.

1. Caudatum Group.	February 26. Per Cent.	March 13. Per Cent.
L2	29.482	27.185
G1	26.018	24.744
A1	26.782	25.810
F1	26.342	27.019
A2	27.491	23.680
F2	27.921	25.065
D	28.275	26.252
2. Aurelia Group.	**February 26. Per Cent.**	**March 19. Per Cent.**
K1	29.473	
I	31.577	31.048
H	31.967	32.102
C2	31.347	31.275
K2	29.416	34.016
g	28.865	28.153

general average for the *caudatum* group is 26.576 per cent.; for the *aurelia* group 30.840 per cent.

In Table XXIV., page 491, we have data for certain other members of the two groups when cultivated under similar conditions. If we determine the ratio of mean breadth to mean length for this table, the results are not so clear as in the cases we have just considered. They are given in Table XXVII.

TABLE XXVII.

Ratio of Mean Breadth to Mean Length for the Races of Table XXIV., page 491.

1. Caudatum Group.	February 5. Per Cent.	February 15. Per Cent.	February 27. Per Cent.
E	31.245	26.158	26.458
D	27.615 25.651	26.010 28.723	26.893
Average	28.170	26.964	26.675
2. Aurelia Group.			
c	26.482	26.396	
g	29.568 30.853	28.298	
i	29.303 29.386	31.852	
Average	29.118	28.849	

In this table the averages for the *aurelia* group are again higher throughout than for the *caudatum* group. But the highest ratio is given by one of the *caudatum* group, and the line *c* of the *aurelia*

group gives in both cases a low ratio. But taking the averages, in connection with those of Table XXVI., it is clear that the smaller races are as a rule slightly broader in proportion to the length than are the larger races.

Turning now to the question whether there are differences in the proportion of breadth to length in different races of the same group, we have full data only for the lines *g* and *i*, as given in Table XXIII., page 488. Beginning with the data for November 23 (since before that date the number of individuals is small), we can make determinations for seven different dates of the ratio of mean breadth to mean length, the two sets being on each date as nearly as possible under identical conditions.

TABLE XXVIII.

Ratio of Mean Breadth to Mean Length for g and i (Table XXIII.).

	November 23. Per Cent.	November 26. Per Cent.	December 7. Per Cent.	December 16. Per Cent.	December 30. Per Cent.	January 2. Per Cent.	February 5. Per Cent.
g	27.011	28.238	34.091	30.370	27.797	27.686	30.853
i	34.291	28.325	34.655	30.159	25.430	24.747	29.386

Thus, in the first three determinations the ratio was greatest in the line *i*; in the last four it was greatest in the line *g*. Evidently there is no constant difference in proportions between these two lines.

For other lines our data are not sufficient to test this matter. Our only positive result on this point then is that the smaller races are as a rule proportionately broader than the larger ones.

2. Results of Selection within Pure Lines.

We have seen that an ordinary "wild" culture of *Paramecium* contains many lines or races, which are differentiated in size. By selection it is possible to isolate these diverse lines; so that in this way we can obtain cultures in which the mean size is large or small, or intermediate, as we prefer. In this case selection, of course, acts by isolating lines that already exist, and allowing them to propagate unmixed.

How do these diverse lines arise? Can we obtain them by selection within the limits of a single line? If from among the progeny of a single individual we select the larger and the smaller specimens,

will we obtain two diverse lines, one showing a greater mean size than the other?

As we have already seen, our first attempts to do this failed. But these first experiments were made before our study of growth and environmental effects, so that the basis of selection was wrong. The smaller specimens selected were as a rule the younger ones; they grew to full size, then, of course, produced progeny of the same size as other adults.

After the thorough study of growth, it appeared possible that a more adequate method of selection might be found. The proportions of the young differ from those of the adult (as our account has shown), so that after long practice one comes to recognize the young specimens with some accuracy. It appeared worth while, therefore, to attempt to select larger and smaller adults for further propagation.

(*a*) *Differences Due to Environmental Action Not Inherited.*

It is, of course, easy to obtain within a pure line adults of different size, by subjecting them to different environments. An analysis of our section on the effects of the environment shows that as a rule these are not inherited. Thus, if we examine Table XVIII. (page 460), we find that the same set that gave on July 17 a mean length of 184.100 microns (row 7) gave one week later, under different conditions, a mean of 146.108 microns; one day later 163.932 microns; one week later 174.400 microns; two days later 191.360 microns. The breadth changed even more, and the extremes of size in a given culture showed corresponding changes. There was no difficulty in changing the dimensions back and forth in the most varied ways. The entire Table XVIII. is an illustration of the general lack of continued inheritance of environmental effects.

Many experiments directed precisely on this point gave the same results. When, for example, the small specimens of row 8 (Table XVIII.) were cultivated under the same conditions as large specimens from row 9, the resulting cultures were soon indistinguishable.

Thus, it is clear that such environmental action as is summarized in Table XVIII. is not as a rule inherited. But I wish to point out and emphasize certain facts regarding the experiments on the action of the environment. (1) In all the experiments thus far tried, the

differential action of the diverse environments lasted but a short time. (2) The experiments were directed toward determining whether the differences produced were *permanently* inherited. Critical investigations have not yet been made to determine whether the environmental effects may not persist for one or a few generations after transference to the new fluid; nor whether long continued action of a certain environment may not produce more lasting results than brief action.

To these points I hope to devote special and extended investigations. The purpose in the present paper is to show on this matter the main general result; this unquestionably is that environmental action is not as a rule inherited in any lasting way.

(*b*) *Selection from Among Differing Individuals in the Same Environment.*

Besides the differences among individuals under different environments, we likewise find differences among individuals of the same pure line in the same culture, as a glance at the tables of the appendix will show. What will be the effect of selecting for breeding larger and smaller specimens from such a culture, avoiding, so far as possible, different stages of growth?

In order to make the selections properly, certain things must be considered. (1) It is well to bring the culture into as stable a condition as possible—a condition where there is little or no multiplication—in order that we may not be confused by different stages in growth. (2) It must be remembered that, so long as conjugation does not occur, the same results that selection would produce are brought about in the ordinary course of events, save that the large and small specimens remain mixed. That is, if there is congenital variation, producing large and small individuals, this must occur in the same way whether the different sizes are isolated or not. The progeny of every individual forms a "pure line," quite unmixed with any other, so long as no conjugation occurs. If, then, by variation a large individual *a* and a small one *b* are produced, and these differences are inherited, then later we shall find a mixture of two strains instead of a single strain. We should then expect the progeny of a

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single individual to show more and more variation as the strain became older; it would break into several or many strains, which would, however, remain intermingled.

Therefore, the best method of procedure will be to take an old strain, which, derived from a single individual, has for a long time been multiplying freely without conjugation. From this the largest and the smallest individuals should be separated and allowed to propagate under identical conditions. If hereditary variations in size have occurred, we should in this way reach the same result as by actual selection and isolation through many generations. Physiological isolation has been as complete as would be experimental isolation.

A race fulfilling these conditions we have in the pure line derived from the individual *D*, on which most of the work described in the first parts of this paper was done. On January 19, 1908, large cultures of *D* had been multiplying without conjugation since April 12, 1907, a period of about nine months. During this time about 250 generations must have been produced; these had remained physiologically isolated. The superfluous individuals had been removed by periodic "catastrophic" destruction; the greater part of the culture was thrown out, and a remnant saved, without selection, for a new culture.

On January 19, 1908, I took from the large stock culture of *D* (1) the ten largest individuals that I could find; (2) the ten smallest individuals I could find. They were separated in two watch-glasses and kept under identical conditions. The difference between the two sets was very marked; the smaller lot were certainly not more than two-thirds the length of the larger, and they were very slender, while the large ones were both long and broad. It was clear that both sets were adults.

It was found that the smaller lot multiplied much less rapidly than the large lot, and some of the small ones died. By January 30 there were but twenty of the small lot, while a very large number had arisen from the large lot. On this date the culture fluid was changed and but fifty of the larger lot retained. The small lot continued to multiply very slowly. It is clear that the small specimens

are weak, sickly ones, and the physiological difference persists at least for some generations (a matter for further study).

On February 5 about half of each lot was killed and measured. This gave 57 specimens from the larger lot, 19 from the smaller. The mean dimensions were, for the larger lot, 169.754 × 46.877 microns; for the smaller lot, 169.895 × 43.579 microns.

Thus the two were practically identical; one could not expect a closer approximation in two identical lots kept separate for seventeen days. The slight difference in breadth is only what we might expect when we consider the extreme sensitiveness of that dimension to faint environmental differences. The most striking differences that we can find as a result of physiological isolation for 250 generations have equalized themselves in a short time, when we got both sets to multiplying freely under the same conditions.

It seems hardly worth while to continue this series, since the two sets have now become equalized. However, they were continued for some time, and samples of 100 each were measured on February 15 and February 27. In these two measurements we find certain differences between the two sets, but these are in opposite directions in the two cases. The means are as follows:

	February 15.	February 27.
Large D	180.240 × 46.880	175.360 × 47.100
Small D	173.240 × 49.760	193.680 × 52.320

Evidently slight environmental differences between the two cultures had crept in. It is clear that the two sets show no constant differences, such, for example, as we find between the two lines, *g* and *i*, in Table XXIII., page 488.

Another set of experiments dealt with the two differentiated lines, *g* and *i*. The line *g* consists of individuals that are constantly larger than those of the line *i*, when the two are under the same conditions (see Table XXIII., p. 488). The experiments consisted in an attempt to separate these races still farther by propagating continually from the largest specimens of *g* and from the smallest specimens of *i*. Thus, if selection is effective, *g* must become larger, *i* smaller. The *length* was the dimension mainly attended to in these selections.

On November 23, 1907, the mean size for *g* was 129.333 × 34.933

microns; for *i* it was 88.268 × 30.268. On this date I placed in separate watch-glasses the ten largest specimens of *g* and the ten smallest specimens of *i*, keeping them under the same conditions.

On November 29 I again selected from the progeny of these the ten largest *g* and the ten smallest *i*, destroying the others.

On December 7 the same selection was repeated; the remainder of each lot was killed and measured. The mean measurements were

g, 120.590 × 41.115 microns.
i, 98.709 × 34.208 microns.

Thus, in spite of the fact that for at least fourteen generations we have selected for propagation the largest of *g* and the smallest of *i*, *g has become smaller and i has become larger!* The results of selection, if there are any, quite disappear in comparison with the effects of slight environmental differences.

In spite of this discouraging result, the experiment was continued. On December 16 I selected the five largest *g* and the five smallest *i* and again measured the rest of each. The results were

g, 127.059 × 38.588 microns.
i, 98.608 × 29.739 microns.

Thus, *i* retains the same length, while *g* has increased, but has not regained the length it had at the beginning of the experiment.

On December 25 the five largest *g* and the five smallest *i* were again selected for propagation.

On December 30, thirty-seven days after the beginning of the experiment, I again measured all but the five largest of *g* and the five smallest of *i*. The results are

g, 112.600 × 30.300 microns.
i, 86.756 × 22.062 microns.

Thus, *i* has decreased as compared with its original length, while *g*, which was selected for increase of size, has decreased a great deal more! The decrease in length of *i* is less than two microns; the decrease in *g* is more than sixteen microns! And this is the result of five selections, taking for *g* the largest, for *i* the smallest, specimens produced in the course of at least thirty generations![8]

[8] The number of specimens on which the measurements are based will be found in Table XXIII., page 488, which includes, for another purpose, the measurements from these experiments.

Evidently, selection is having no effect that can be detected. The fluctuations in the two sets are precisely what would be expected from unavoidable changes in conditions of nutrition; they show no relation to selection.

Later another experiment in selection was tried with these same races, *g* and *i*. On January 19 I selected from a large culture that had been multiplying freely for a month (1) the ten largest specimens of *g* that I could find; (2) the ten smallest specimens of *g*; (3) the ten largest specimens of *i*; (4) the ten smallest specimens of *i*.

These were allowed to multiply under identical conditions till February 5. Then a sample of fifty of each was measured. The results are as follows:

Large *g*, 114.720 × 33.920 microns.[9]
Small *g*, 116.912 × 36.070 microns.
Large *i*, 92.000 × 26.960 microns.
Small *i*, 93.583 × 27.500 microns.

The difference between the two sets of each is slight and without significance, but such as is found is in favor of the progeny of the *smaller* specimens in each case.

Evidently, we are not making a start with any effect of selection, and it is useless to continue the experiment.

Many other attempts were made to break a pure line by selection into several strains; on this point an immense amount of work was directed. But in most cases the difference between the two sets became equalized almost at once, so that the experiments were not carried farther. As soon as two unequal sets become quite equalized, there is little opportunity for further selection. In the experiments described above, though their futility seemed evident from the first results, the work was continued for many generations, in order that failure might not be due to lack of perseverance.

One other set of experiments deserves to be described, because in these the basis for selection was changed. Among the progeny of a certain individual *Nf2* conjugation occurred. The conjugants varied in size. This offered an opportunity to make a selection

[9] These measurements are found, for another purpose, in Table XXIV., page 491.

based on specimens that were evidently adults; possible confusion due to growth differences could be avoided.

On March 31 I killed and measured all but the largest and smallest pairs of conjugants; the length was found to vary from 124 to 148 microns. The smallest and largest pairs were reserved for propagating; the former, of course, measured not more than 124 microns, the latter not less than 148 microns. These were allowed to multiply separately, but under the same conditions, till April 10.

On April 10 I measured a random sample of 100 specimens of the progeny of each of these pairs. The results are as follows:

Larger pair, 151.920 × 43.840 microns.
Smaller pair, 158.760 × 38.120 microns.

Thus, the difference in size, whatever its cause, does not correspond to the difference between the ancestors; selection for size has had no evident effect.

Another experiment on the progeny of *Nf2* consisted in comparing the descendants of a single small conjugant with those of several large non-conjugants. Details of this and similar experiments will be reserved for our paper on the relation of conjugation to variation and heredity. But since it has a certain bearing on our present problem, the results may be given here.

At the same time with the cultures last described (on March 31), I isolated ten of the largest non-conjugant progeny of the same individual *Nf2*. A sample of thirty-four of these had given a mean length of 147.412 microns, so that this may be taken as the mean length of these ten specimens. With the progeny of these was compared the progeny of the smaller pair mentioned in the preceding experiment. As we have seen, this pair measured not more than 124 microns in length. The greatest pains were taken to cultivate the two sets under identical conditions. On April 20 I killed a sample of 108 of each. The mean measurements were as follows:
Progeny of small pair (124 microns) — 160.852 × 42.036 microns.
Progeny of ten large (147 microns) — 156.482 × 43.815 microns.

Thus, again, there is no correspondence between the differences in size of the parents and those of the progeny. The determining factor in the size is the fact that both sets belong to the same pure

line; the variation of the parents from the type of the pure line has no effect. The difference in the figures above is either purely statistical in character or means a faint variation in the culture fluid.

(*c*) *Summary on Selection within Pure Lines.*

Thus, we come uniformly to the result in all our experiments, that selection has no effect within a pure line; the size is determined by the line to which the animals belong, and individual variations among the parents have no effect on the progeny.

But for our results with different lines, it might be maintained that the reason why we get no constant differences between the progeny of different individuals of the same line is because the effects of environment are so much greater than the effects of selection that the latter are covered up and obscured. But as soon as we are dealing with lines that are really different (though by but a small amount) we have no such difficulty; the different lines retain their relative sizes in spite of environmental action. This is clearly shown in Tables XXIII. and XXV., pages 488 and 494.

The significance of these results will be dealt with in the next section.

VI. SUMMARY AND DISCUSSION.

1. Résumé of the Investigations.

The present paper is an experimental study of the factors involved in variation and inheritance of size in the infusorian *Paramecium*, in the period when reproduction is taking place by fission, without conjugation.

1. The first question proposed is whether the differences in size among different individuals of a culture are inherited. The preliminary study showed that in a typical culture there were two permanently differentiated groups of large and small individuals, respectively, corresponding to what had been described as the two species, *Paramecium caudatum* and *Paramecium aurelia*. But when a culture was produced from a single individual of either of these groups, forming thus a "pure line," it was found that though the different individuals of the single pure line differed much in size,

these differences were not inherited. Large and small specimens of a single pure line produced progeny of the same mean size.

2. The next question then was: What are the causes and the nature of the variations in size among the different individuals of a culture of *Paramecium?* Even in a pure line the individuals differ greatly. The "polygon of variation" of a given culture was looked upon as a mass of problems for analysis. What determines the position which any given individual holds in such a polygon, or in a correlation table? And why do different lots of *Paramecia* differ in mean dimensions; in the amount of variability; in proportions, and in the correlation between length and breadth?

The analysis of the factors in variation led to a detailed study of (1) growth, (2) the effect of the environment; (3) inherited differences in size. To these three matters the three main divisions of the paper are devoted. To one or the other of these three categories most of the variations in size were found to belong. A fourth category, consisting of variations connected with conjugation, is reserved for consideration in a later paper.

3. A large share of the differences in size to be observed in a given culture are differences in growth. In study of variation in protozoa it is as necessary to take growth into consideration as it is in the study of higher animals; the part played by it is fully as great in the protozoa as elsewhere. The paper gives a detailed study of growth, based on the measurements of 1,500 specimens of various known ages, in comparison with large numbers of "random samples." In this way a curve of growth was plotted (Diagram 5, page 449); this curve resembles essentially the curves of growth of higher animals, as the rat, or man. In different parts of this curve of growth individuals show different lengths, different breadths, and, of course, different proportions of breadth to length. A flourishing culture contains individuals in all stages of growth; so that this affects largely the mean dimensions, the observed variations, and the correlations between length and breadth. The precise effects of growth on each of these matters are dealt with in detail in the paper; they will be summarized in later paragraphs. A summarized account of growth and its effects is found in the body of the paper, pages 447 to 458; the constants for dimensions and variation in dif-

ferent stages of growth are brought together in Table X., page 428.

4. Environmental conditions were found to play a very large part in determining dimensions, variations and correlation in *Paramecium*. Conditions of nutrition were found to be particularly effective. By changes in nutrition the mean length of a given culture could be changed in a week from 146 microns to 191 microns; the breadth from 31 to 54 microns; in twenty-four hours the coefficient of variability for length was thus changed from 7.003 to 12.767, for breadth from 12.473 to 28.879; the coefficient of correlation from .3906 to .8463. Changes of the most varied sort could be produced and reversed with the greatest ease in short periods; many examples of this are summarized in Table XVIII., page 460. Within a given culture at a given time many of the differences between individuals are due to slight environmental differences in different regions. The breadth is more sensitive to environmental changes than the length; to such an extent is this true that it is difficult to use the breadth dimensions for accurate study of any other factors. A summary on the effects of the environment on dimensions, proportions, variation and correlation is found on pages 476 to 484.

5. After the study of growth and environmental action, an investigation was made of the internal factors in dimensions and variation; of the inheritance of size. Are all the observed differences between the individuals of a culture mere matters of growth and environment? Or may we find different races or lines that retain their relative sizes even in the same stage of growth and in the same environment?

A thorough experimental study showed that a given "wild" culture usually contains many different lines or races, which maintain their relative sizes throughout all sorts of changing conditions. Eight of these differing pure lines were isolated and propagated; these varied in mean length from a little less than 100 to a little more than 200 microns (see Tables XXIII. and XXV.). Other lines could unquestionably be distinguished by sufficiently accurate experimentation.

These different lines fall usually into two main groups, one group having a mean length greater than 170 microns, the other having a mean length below 140 microns. These two groups correspond to

the distinction that has been made between two species, the larger ones representing the supposed species *caudatum*, the smaller ones *aurelia*. But a line or race was found with mean length lying midway between these groups, at about 150 to 160 microns.

The smaller or *aurelia* lines were found to be, under the same conditions, as a rule a little broader in proportion to the length than the larger or *caudatum* lines. But the difference is slight and the two sets overlap extensively in this matter; slight differences in environment quite obscure the difference in proportions.

The differences among the different lines were found not to be due to different periods of the life cycle. By beginning with conjugating pairs of different sizes, distinct pure lines were as readily isolated as by beginning anywhere else in the cycle.

6. After becoming thoroughly familiar with differences due to growth, to environment, and to divergent ancestry, a further attempt was made to change by selection the characteristics of pure lines, or to break such lines into strains of differing size. In spite of much work directed on this point, it was found that selection within a pure line was quite without effect. Large individuals of the line produce progeny of the same mean size as do the small individuals. To this matter we return in later paragraphs.

2. Determining Factors for Dimensions, Variations and Correlations.

Based on the analysis of the factors in variation above set forth, a summary can be given of the various determining causes of the different dimensions, the proportions, the amount of variation and the correlations observed in samples of different cultures of *Paramecium*. We may take as an example such a sample as is shown in Table LXI. (appendix) from a "wild" culture.

1. The various different *lengths* depend upon the following factors:

(*a*) The collection embraces a number of different races or lines, having different lengths even when all conditions are the same. We have seen that different lengths varying from less than 100 to more than 200 microns may be included as a result of this fact. The *mean* length may not represent any of these races (this is the case in Table I.).

(*b*) The collection includes various growth stages of each of the lines represented. The youngest stages of each line are little more than half the lengths of the adults; all intermediate stages may be present, and the adults themselves shorten again as they approach fission. A very wide range of variation in length may be brought about by these growth stages, all within the limits of a single pure line or race. Of course when many different lines are present, an immense number of combinations are thus produced.

(*c*) The collection includes individuals of the various races that have lived under slight or considerable differences in environment, particularly in the matter of nutrition. Those that have been able to get more food will be much larger and will multiply more frequently (thus giving more young) than those that get less. Even slight environmental differences make decided differences in dimensions. While the environment shows its effects most strongly on comparison of different cultures, even within the same culture, and when all the individuals are of one race and of approximately the same age, there are marked differences due to this cause. This is shown, for example, in Table XLI. (appendix); here variations in length from 140 to 200 microns must be considered environmental effects. A few drops of water form a varied microcosm to the infusoria. When diverse pure lines, diverse growth stages, and diverse environmental conditions are found in a culture (as is usually the case), of course, the number of different sizes and forms due to the varied combinations of all these factors are very great. The same sizes may, of course, be produced in different ways; two diverse lines in different stages of growth or in different environments, or in some combination of the two, may produce forms outwardly identical. The actual variety, as defined by the physiological conditions, is therefore much greater than the measurements show, for the latter throw together heterogeneous combinations.

Combinations of all the three factors inducing diversity might give us in a single collection individuals varying in length from 50 microns to 332 microns. While these are the extremes given by our data, presumably the actual extremes would be still more divergent.

(*d*) In different collections the observed *mean* lengths depend upon the three different sets of factors just mentioned. The inclu-

sion of different *lines* or *races,* even if conditions of growth and environment are essentially the same, may give us, as we have seen, mean lengths of somewhat less than 100, or somewhat more than 200 microns, or any intermediate length. Different *stages in growth* may give us, in the same line and in the same environment, means differing to such an extent that one is nearly twice the other, or any intermediate condition. The absolute extreme values will, of course, depend upon the race employed; in the line *i* the variation of mean length caused by growth might be from about 50 to about 100 microns; in *D* it was from about 100 to about 200 microns; in *L* it would be from about 117 to 234 microns. Different *environmental conditions* give us, within the same lines, mean lengths differing to such an extent that the greater is 25 to 30 per cent. more than the less (lines *c* and *D*). In different "wild" cultures we shall have different combinations of all these factors, resulting in extreme diversities in different cases. Fig. 7 shows two extreme sizes drawn to the same scale (page 496).

2. The various different breadths depend upon the same factors as the different lengths. There are certain differences, however. As compared with length, the breadth is affected much less by growth; about the same (though a trifle less) by diversity of race; and much more by environmental differences. Environmental differences produced within the races *D* and *c* such differences in mean breadth that the greater was about twice the less.

3. The observed variation, as measured by the coefficient of variation, of course, depends upon the three sets of factors enumerated above as affecting the length and breadth. If a collection consisted of several different lines or races, all in the same condition as regards growth and environmental conditions, this would, of course, give us a considerable coefficient of variation. For example, if a collection consisted of ten individuals each of all the different lines represented in Table XXVI., page 502, and if all of each set of ten had the mean dimensions for its line (thus excluding differences due to growth and environment within the lines), the coefficient of variation when computed in the same way as for the actual collections given in the text is found to be for length 19.689; for breadth 15.679.

If a collection consists of individuals all belonging to the same

line or race, and in the same environment, then the coefficient of variation depends largely upon the stages of growth it contains. By taking specimens nearly in the same stage of growth we were able to reduce the coefficient of variation in length in some cases to 4.521, in breadth to 6.976, while by taking collections including various ages, under similar conditions, coefficients were found as high as 13.729 for length and 13.292 for breadth (Table X.). The most carefully selected lots contain specimens differing a certain amount in age, otherwise the coefficient of variation could be still further reduced in this way. Specimens beginning fission or undergoing conjugation include few growth stages, hence they show a low coefficient of variation. The coefficient for those beginning fission is less than for conjugants (see page 453).

The coefficient of variation for a given line is tremendously affected by environmental conditions. Thus, we see this coefficient changed in twenty-four hours, by a change in environment, from 7.003 to 12.767 for length; from 12.473 to 28.879 for breadth. Different environments give us all sorts of values between such extremes.

It is evident that no particular coefficient of variation can be considered characteristic of *Paramecium,* or of any line of *Paramecium;* certainly not unless the conditions as to growth, environment, etc., are very precisely defined. We have seen that the variations found among different individuals of the same pure line *do not show themselves to be heritable.* This, along with all the rest of the evidence, indicates that if all conditions of growth and environment were made identical throughout a sample of *Paramecia* belonging to a pure line, the coefficient of variation would be very near to zero. In other words, all the variations that we have been able to detect with certainty in a pure line are due to growth and environment. Presumably other variations (congenital and hereditary) must occur at times, but they appear to be so rare that it is difficult to detect them and they would have little effect on the coefficient of variation. By properly varying the conditions, we may get in a pure line all coefficients of variation in length, from a limit near zero up to 20 or more.

4. The ratio of breadth to length (serving to partly define the

form of the body), of course, varies in dependence upon all the three sets of factors with which we have dealt—difference of race, growth and environmental conditions. The smaller races are found to show, under the same conditions, a slightly greater ratio of breadth to length (see Table XXVI.). Within the same race different stages of growth show different ratios; in general, the proportion of breadth to length is greatest in the young, and gradually decreases with age; it increases again very rapidly in preparation for fission. Environmental agents affect in most marked and varied ways the proportion of breadth to length; this is connected with the fact that such agents act more upon the breadth than upon the length. A detailed summary of the different effects of the environment on the proportion of breadth to length is found on pages 478 and 479. The most important general relation is, that increase of nutriment increases the proportional breadth; decrease of nutriment produces the opposite effect. Any agent which suddenly increases the breadth likewise, as a rule, increases the ratio of breadth to length.

5. The coefficient of correlation between length and breadth is the measure of the accuracy with which breadth and length vary proportionately. If the proportion of breadth to length is the same in all individuals of a collection, then the coefficient of correlation of that collection is 1.000.[10] Since, as we have just seen, the proportion of breadth to length is altered by many factors, it follows that all these factors modify the correlation, tending to reduce it below 1.000. The correlation is affected by all the three categories of factors that affect the dimensions in essentially the following ways:

(*a*) The inclusion of different races in a collection, particularly if some of the smaller and some of the larger races occur, makes the correlation less than 1.000, because the proportion of breadth to length is greater in the smaller races. The reduction in correlation produced by this alone is very slight. If we make a collection by

[10] It is perhaps not necessary to point out that the "coefficient of correlation" is *descriptive;* it shows the observed condition in a given set of measurements. The *cause* of this condition is a matter to be determined. *Correlation* is often conceived physiologically as an underlying something that binds two things together, so that they must change correspondingly. The descriptive correlation of the statistician may be the resultant of many factors.

throwing together ten each of the different lines of Table XXV. (page 494), giving the individuals of each line the mean dimensions of its line (thus nearly excluding variations due to growth and environment), then calculate the coefficient of correlation in the same way as for our other collections, we find it to have the high value of .9735.

(*b*) The inclusion of different stages of growth in a collection reduces the correlation below 1.000, since different growth stages have different ratios of breadth to length. A detailed summary of the effects of growth on correlation is found on pages 455 to 457; here we can notice only the main points. In the earliest stages of growth the length is increasing while the breadth is decreasing; hence if we take a collection including various stages within this period, the correlation between length and breadth becomes negative; it may fall to a value of —.3138 (see Table X.). The inclusion of various early stages in a collection of adults decreases the positive correlation shown by the adults. In later growth, length and breadth increase together; the inclusion of various stages at this period has little effect on the correlation; it does, however, tend to reduce it slightly, since length and breadth do not increase at the same ratio. In old specimens, beginning fission, the length decreases while the breadth increases; a collection including different stages in this process tends again to give negative correlation, or to reduce the positive correlation due to other causes. In a collection from the same pure line, in which all specimens are in the same stage of growth, the correlation between length and breadth is high; this would be true no matter what stage of growth is the one represented. Random samples from any culture usually contain many stages of growth; this lowers the correlation between length and breadth.

(*c*) Environmental differences, like growth, affect length and breadth differently or in different proportions; if individuals thus diversely affected are included in a sample, this tends to decrease the correlation between length and breadth. A detailed analysis of the many and important effects of environmental action on the correlation will be found on pages 481 to 484; here, again, we can but summarize the important points.

1. Certain environmental agents increase the breadth while decreas-

ing the length. Inclusion of different stages of this process in a sample reduces the correlation; it may make it zero or negative.

2. Most environmental agents change the breadth more than the length, even when both are changed in the same direction The inclusion of different stages then reduces correlation.

3. Samples in which some of the specimens are well-fed and plump, others ill-fed and thin, of course, show low correlation, since the ratio of breadth to length is not uniform. This is usually the case in cultures where food is scarce.

4. Addition of abundant nutriment causes the thin specimens to increase in breadth, by taking food, while the plump ones change little. As a result the proportion of breadth to length becomes nearly uniform throughout the lot; the correlation is therefore increased. As a rule, any agent which increases the mean breadth likewise (for the reason just set forth) increases the correlation between breadth and length.

Decrease of nutriment, for the converse reason, decreases the correlation.

5. Any agent that causes rapid multiplication decreases the correlation between length and breadth for the period of multiplication. This is owing to the inclusion in the collection of many stages of growth, showing different proportions of length to breadth.

6. Slight differences in one dimension may be produced without corresponding differences in the other, so that in a collection varying little in length the correlation may be low. But considerable changes in one dimension are usually accompanied by corresponding changes in the other. Hence, when two groups of differing lengths are thrown together, the correlation may become higher than in either one taken separately (for example, see page 437).

In any ordinary sample of *Paramecium* all these varied factors are at work in determining the observed correlation. It is clear that no particular coefficient of correlation can be considered characteristic for *Paramecium* or for any particular race of *Paramecium*, for by various combinations of these factors we may get any coefficient of correlation ranging from a pronounced negative value upward through zero to a high positive value. In Tables X. and XVIII. we

see varied collections showing extremes of value for the coefficient of correlation, from —.3138 to +.8500.[11]

3. Results on Variation, Inheritance and the Effects of Selection.

Our general results with regard to variation, inheritance and the effects of selection are then as follows:

In a given "pure line" (progeny of a single individual) all detectible variations are due to growth and environmental action, and are not inherited. Large and small representatives of the pure line produce progeny of the same mean size. The *mean size* is therefore strictly hereditary throughout the pure line, and it depends, not on the accidental individual dimensions of the particular progenitor, but on the fundamental characteristics of the pure line in question.

In nature we find many pure lines differing in their characteristic mean dimensions.

Our results with the infusorian *Paramecium* are, then, similar to those reached recently by certain other investigators working with pure lines of other organisms. Johannsen (1903) showed that in beans and in barley many pure lines, slightly differentiated from each other, exist in nature, but that selection within a pure line has no effect upon its characteristics. These plants are self-fertilized, so that there is no intermingling of different lines. Hanel (1907) has recently found the same state of affairs in *Hydra* when multiplying by budding. Certain lines tend to have a higher mean number of tentacles, others a lower mean number. But within a given line selection of parents with more or fewer tentacles has no effect on the progeny; selection has no effect within the pure line.

It is doubtless too early to draw any very positive conclusions from these facts. While the results with *Paramecium* seem clear, I intend to test them further in every way possible. It is possible that selection may be made on some other basis, with a better

[11] This fact of course does not render the study of the coefficient of correlation valueless. Its examination under varied experimental conditions is of the utmost importance for determining the real effects of various agents, and in many other ways it furnishes a valuable datum.

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chance of avoiding differences due to environment and growth. It is conceivable that congenital hereditary variations exist, but that they are few in number compared with those due to environment and to slight differences in ways of living, so that in our selection we always get the mere environmental variations. There are decided differences between the specimens of the same line beginning fission, as Table XIII. (page 442) well shows; here the length varied from 156 to 204 microns. It is possible that selection among specimens beginning fission might have a better chance for success. I have attempted this, but it is extremely difficult; I hope to return to it.

We must consider, however, that if the non-inheritable differences are so much more numerous and marked than the inheritable ones as to render conscious selection by human beings ineffective, they would apparently have the same effect on selection by the agencies of nature. The same ground for selection offered by heritable variations is offered so much more fully by those not heritable that there would be as little effect in selection by nature as in selection by man.

Certainly, therefore, until someone can show that selection is effective within pure lines, it is only a statement of fact to say that all the experimental evidence we have is against this. The results set forth in the present paper tend to strengthen that explanation of the observed facts regarding selection, regression, etc., in mixed populations, which is set forth by Johannsen (1903). We need not discuss these in detail here; they are essentially as follows:

1. Selection in a mixed population consists in isolating the various different lines already existing.

2. If selection is made, not of single individuals, but of considerable numbers having a certain characteristic, then by repeated selection it will be possible to approach nearer and nearer to a certain end.

Thus, if we select from such a heterogeneous collection as is represented in Table LXI. all the larger individuals, we shall have taken representatives of many different lines. Our selection will include the larger individuals of lines of median size, as well as the average individuals of lines of large size. The progeny of this selected lot will then consist of various lines, some larger, some smaller, but with the average higher than in the original collection. Another selection

will raise the average still further by getting rid of some of the smaller lines, etc.

3. It has been noticed that in many cases continued selection will not carry a character beyond a certain point. This is due (on the view we are setting forth) to the fact that we have finally isolated that line (or lines) of the original collection which had this character most strongly marked, and since selection of the fluctuations has no effect within the pure line, we can make no farther progress.

4. The phenomenon of so-called *regression* finds its explanation in the same way. It is found that when extremes are selected, the progeny of these extremes stand nearer the mean than did the parents, though they diverge in the same direction as the parents. The reason for this may again be seen by considering such a heterogeneous collection as that of Table LXI., with the effects of selecting the extremes of size. If we select the largest and the smallest individuals, we shall have taken (1) the largest individuals of the largest lines, and (2) the smallest individuals of the smallest lines. But these, when they propagate, produce, as we have seen, merely the *means* of the lines to which they belong. The largest individuals will produce then progeny that average smaller than themselves; the smallest individuals progeny that are larger than themselves; both sets will then approach the mean of the original collection as a whole.

In working with populations reproducing by cross fertilization among the different lines, the conditions on which these results depend become quite obscured, owing to the introduction of new factors, the union of different factors, the appearance of mendelian results, etc. Work with pure lines perhaps shows the real cause for the observed phenomena above set forth.

It must be admitted, then, that the work with pure lines, indicating that selection of fluctuations within the lines is powerless, leads to a simple and consistent explanation of many of the observed facts. But, of course, it gives no explanation of the origin of the different pure lines. Clear proof of the effectiveness of selection even within a pure line would therefore be of the greatest interest, and the present writer would find great pleasure in being the first to present such proof. But until such proof is forthcoming, it must be

admitted that the experimental results go strongly against the effectiveness of selection among slight fluctuating variations in producing new inherited characteristics.

How, then, do the different pure lines rise? This is after all the main problem. Toward its solution further investigations of this series will be directed. It is proposed to study in detail (1) the effects of conjugation on variation, heredity and the production of new races; (2) the effects of long-continued differences in environmental action on different divisions of the same line; (3) the question whether the different lines arise from something like mutations. Further, (4) additional different way of exercising selection within a single line will be tested. The question may be raised whether the production "by mutation" of such slight differences in size as we are here dealing with would not be essentially the same as their production by the inheritance of slight variations—since the extent of the "mutations" would not be greater than what we should call slight variations in size. The difference between the two conceptions almost or quite vanishes when we come to deal with such minute changes in characteristics as those we find in the different lines of *Paramecium*. The "mutation" would be merely a *rare*, heritable, variation, and it is now clear that heritable variations in size are much rarer than had been supposed; their number is so small that in *Paramecium* they are not statistically detectible among the many non-heritable fluctuations due to the environment.

RAQUETTE LAKE, NEW YORK,
August 22, 1908.

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APPENDIX.

Tables of Measurements.

The first twenty-eight tables are distributed through the text. Tables XXIX. to LXIII. follow.

Table XXIX.

Correlation Table for Length and Breadth of 59 Specimens, Age 0 to 5 Minutes. (See Lot 2, Table 10.) Descendants of *D.*

Length in Microns.

Breadth in Microns.	76	80	84	88	92	96	100	104	108	112	116	120	124	128	132	
36										1						1
40						1	1	1				2	1			6
44					2		4	1	2		5	1	3	2	1	21
48			1	2	3	1	3	1	2	2		1	2	1	1	20
52	1	1			3				1		1	1	1		1	10
56	1															1
	2	1	1	2	8	2	8	3	5	3	6	5	7	3	3	59

Length—Mean, 107.660 ± 1.296μ Breadth—Mean, 46.372 ± .332μ
St. Dev., 14.780 ± .916μ St. Dev., 3.804 ± .236μ
Coef. Var., 13.729 ± .868 Coef. Var., 8.200 ± .524

Mean Index, 44.037 per cent.; Coef. Cor., —.3138 ± .0792.

Table XXX.

Correlation Table of Length and Breadth for a Random Sample of Lot 2, Table X.—Same Lot from which came Specimens in Tables VII. and XXIX. Descendants of D. (24 hours in fresh hay infusion: July 17.)

Length in Microns.

Breadth in Microns.	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	
36	1				1	2	1		1	1			1								8
40				1	2	5	4	3	3	5	6	3	6	3	1	1					43
44			2	1	1	3	1	2	4	5	3	7	7	4	7	6	3		1		57
48					1	2	2	3	3	2	3	1	2	9	2	4	5	3	1		43
52					1	1	1		2			3	2	6	4	4	1	2	3	2	32
56					1	1			1		2	1			3	2	2	1		1	15
60																	1	1			2
	1	0	2	2	7	14	9	8	14	13	14	15	18	22	17	17	12	7	5	3	200

Length—Mean, 184.100 ± .776μ Breadth—Mean, 46.020 ± .251μ
St. Dev., 16.264 ± .548μ St. Dev., 5.256 ± .177μ
Coef. Var., 8.834 ± .300 Coef. Var., 11.421 ± .390

Mean Index, 25.084 per cent.; Coef. Cor., .4282 ± .0389.

TABLE XXXI.

Correlation Table for the Length and Breadth of the Young of Lot 6, between the Ages of 0 and 19 Minutes. (See Table X., row 7.)

Length in Microns.

Breadth in Microns.	108	112	116	120	124	128	132	136	140	144	148	152	
52		1							2				3
56	1	1	1	1	1		1						6
60	2							1	3	1		1	8
64				1				1	1		1		4
68			1										1
72						1							1
76		1											1
	3	3	2	2	1	1	1	2	6	1	1	1	24

Length—Mean, 128.000 ± 1.908μ
St. Dev., 13.856 ± 1.348μ
Coef. Var., 10.825 ± 1.066

Breadth—Mean, 60.168 ± .788μ
St. Dev., 5.712 ± .556μ
Coef. Var., 9.495 ± .933

Mean Index, 47.573 per cent.; Coef. Cor., — .0337 ± .1375.

TABLE XXXII.

Correlation Table for Length and Breadth of Young of Lot 7, between the Ages of 0 and 19 Minutes, Descendants of Individual D. (See Table X., row 13.)

Length in Microns.

Breadth in Microns.	108	112	116	120	124	128	132	136	140	144	148	152	156	160	
36												1			1
40						1		1				1			3
44		3		1	2	1				1	1	1	1	1	12
48			1	1	2	1			1	1	4	2		1	14
52	1	1		1	3	1	1					1			9
	1	4	1	3	7	4	1	1	1	2	5	6	1	2	39

Length—Mean, 134.256 ± 1.663μ
St. Dev., 15.394 ± 1.176μ
Coef. Var., 11.468 ± .857

Breadth—Mean, 46.768 ± .408μ
St. Dev., 3.792 ± .288μ
Coef. Var., 8.109 ± .623

Mean Index, 35.643 per cent.; Coef. Cor., — .2546 ± .1010.

TABLE XXXIII.

Correlation Table for Length and Breadth of Young of Lot 6, between the Ages of 18 and 28 Minutes. (See Table X., row 8.)

Length in Microns.

Breadth in Microns.	132	136	140	144	148	152	156	160	
48				5					5
52		4	6	7	2	1	2		22
56	2	4	3	2	1	1			13
60		1	2		1	1	1	1	7
64					1		1		2
	2	9	11	14	5	3	4	1	49

Length—Mean, 143.348 ± .624μ Breadth—Mean, 54.284 ± .364μ
St. Dev., 6.480 ± .440μ St. Dev., 3.788 ± .260μ
Coef. Var., 4.521 ± .309 Coef. Var., 6.976 ± .478

Mean Index, 37.921 per cent.; Coef. Cor., 1937 ± .0927.

TABLE XXXIV.

Correlation Table for Length and Breadth of 106 Specimens, Age 18–28 Minutes. (See row 15, Table X.) (Descendants of *D*, but taken part one day, part another.)

Length in Microns.

Breadth in Microns.	112	116	120	124	128	132	136	140	144	148	152	156	160	164	168	
36	1															1
40									1							1
44				1	2	1			1	3	2	1	2	1		14
48						1	1	6	16	3	3	2			1	33
52						1	5	6	8	3	4	3	1			31
56						4	4	3	2	3	1					17
60							1	2		1	1	1	1			7
64										1		1				2
	1	0	0	1	2	7	11	19	29	13	10	9	3	0	1	106

Length—Mean, 143.812 ± .544μ Breadth—Mean, 50.832 ± .320μ
St. Dev., 8.296 ± .384μ St. Dev., 4.900 ± .228μ
Coef. Var., 5.769 ± .268 Coef. Var., 9.640 ± .451

Mean Index, 35.438 per cent.; Coef. Cor., 1319 ± .0644.

TABLE XXXV.

Correlation Table for Length and Breadth of Young of Lot 6, between the Ages of 35 and 45 Minutes. (See Table X., row 9.)

Length in Microns.

Breadth in Microns.	132	136	140	144	148	152	156	160	
48				1	1	1			3
52	1		1		1	1	1	1	6
56			2	1	2	1	1	2	9
60			1			1		1	3
64					1	1	1	1	4
	1	0	4	2	5	5	3	5	25

Length—Mean, 149.920 ± 1.012μ Breadth—Mean, 55.840 ± .636μ
St. Dev., 7.512 ± .716μ St. Dev., 4.724 ± .452μ
Coef. Var., 5.010 ± .479 Coef. Var., 8.461 ± .813

Mean Index, 37.296 per cent.; Coef. Cor., .2799 ± .1243.

TABLE XXXVI.

Correlation Table for Length and Breadth of Young of Lot 6, between the Ages of 75 and 90 Minutes. (See Table X., row 10.)

Length in Microns.

Breadth in Microns.	140	144	148	152	156	160	164	168	172	176	180	
40	1											1
44												0
48	1		2	1	1		1	1	1			8
52			1	2	6	1	4		1		1	16
56				1			4			1		6
60						1	2	1	1	2	1	8
64												0
68						1	1		1			3
	2	0	3	4	7	3	12	2	4	3	2	42

Length—Mean, 161.524 ± 1.004μ Breadth—Mean, 54.192 ± .600μ
St. Dev., 9.648 ± .712μ St. Dev., 5.752 ± .424μ
Coef. Var., 5.974 ± .441 Coef. Var., 10.617 ± .790

Mean Index, 33.558 per cent.; Coef. Cor., .5232 ± .0756.

TABLE XXXVII.

Correlation Table for Length and Breadth of Young of Lot 9, between the Ages of 3 and 4 Hours. (See Table X., row 16.)

Length in Microns.

Breadth in Microns.	132	136	140	144	148	152	156	160	164	168	172	176	
40					1								1
44		1	1	3	1	2			1				9
48	2	1	9	1	3	3	4	3		1			27
52		5	6	4	3	2	3	4	1	1	1		30
56			3	2	1	3	3	3	2				17
60				2		1	1			1		1	6
64							1		2				3
	2	7	19	12	9	11	12	10	6	3	1	1	93

Length—Mean, 149.636 ± .688μ Breadth—Mean, 51.568 ± .322μ
St. Dev., 9.856 ± .488μ St. Dev., 4.752 ± .236μ
Coef. Var., 6.587 ± .327 Coef. Var., 9.212 ± .459

Mean Index, 34.546 per cent.; Coef. Cor., .3201 ± .0628.

TABLE XXXVIII.

Correlation Table for the Length and Breadth of Young of Lot 9, between the Ages of 4.20 and 5 hours. (See Table X., row 17.)

Length in Microns.

Breadth in Microns.	164	168	172	176	180	184	188	192	196	200	204	208	212	216	
52		1	1	4	2	2	1								11
56	1	2	1	2	5	5	5	3	1		1				26
60		1		2	4	3	4	2	3	3	1				23
64				1	3	3	7	6	1	2	1				24
68					1		1	1	2	1					6
72									1	2				1	4
76										1					1
	1	4	2	9	15	13	18	12	8	9	3	0	0	1	95

Length—Mean, 186.736 ± .652μ Breadth—Mean, 60.168 ± .360μ
St. Dev., 9.416 ± .460μ St. Dev., 5.224 ± .256μ
Coef. Var., 5.043 ± .247. Coef. Var., 8.679 ± .428

Mean Index, 32.225 per cent.; Coef. Cor., .5557 ± .0478.

TABLE XXXIX.

Correlation Table for Length and Breadth of Paramecia at the Age of 12 Hours. (Descendants of *D;* See Table X., rows 20 and 21.)

Length in Microns.

Breadth in Microns.	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	
48	1							1														2
52		1								1												2
56									1	1	1	3	2		1	1	2					12
60											2	1	2	2	2	1	4	1				15
64											1		2	3	5	4	2	3			1	21
68														4	3	3	2	1				13
72													1	5		1						7
76																						0
80															1							1
	1	1	0	0	0	0	0	1	1	2	4	4	7	14	12	10	10	5	0	0	1	73

Length—Mean, 188.988 ± .996μ Breadth—Mean, 62.796 ± .464μ
St. Dev., 12.612 ± .704μ St. Dev., 5.872 ± .328μ
Coef. Var., 6.672 ± .374 Coef. Var., 9.350 ± .526

Mean Index, 33.275 per cent.; Coef. Cor., .4868 ± .0602.

TABLE XL.

Correlation Table for Length and Breadth of Paramecia at the Age of 18 Hours. (Descendants of *D;* See Table X., row 22.)

Length in Microns.

Breadth in Microns.	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	228	
48			1	2	1						1						5
52	1	1		1	1	5	2	6	5	4	3	1	1				31
56		1		1	4	2	4	6	5		2	5					30
60				2	1			1	5	4	4	2	5	1		1	26
64						1		1	1	4	1	1		2			11
68											2						2
	1	2	1	6	7	8	6	14	16	12	13	9	6	3	0	1	105

Length—Mean, 199.048 ± .780μ Breadth—Mean, 56.496 ± .292μ
St. Dev., 11.844 ± .552μ St. Dev., 4.428 ± .208μ
Coef. Var., 5.949 ± .278 Coef. Var., 7.837 ± .367

Mean Index, 28.427 per cent.; Coef. Cor., 4304 ± .0536.

TABLE XLI.

Correlation Table for Length and Breadth of 300 Paramecia at the Age of 24 Hours. (Descendants of *D;* See Table X., row 23.)

Length in Microns.

Breadth in Microns.	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	
28	1		2	1	1												5
32	1	4	2	5	8	8	7	6	2								43
36				5	8	8	9	15	10	7	2	1			1		66
40			1	2	5	3	10	16	12	7	9	3	1				69
44		1		1	2	6	9	10	12	7	6	6	4		1		65
48					2	2	4	3	1	8	6	3	6			1	36
52								2		3	3			2			10
56							1		2			1	1	1			6
	2	5	5	14	26	27	40	52	39	32	26	14	12	3	2	1	300

Length—Mean, 168.532 ± .419μ Breadth—Mean, 40.320 ± .230μ
St. Dev., 10.768 ± .296μ St. Dev., 5.892 ± .162μ
Coef. Var., 6.389 ± .175 Coef. Var., 14.615 ± .411

Mean Index, 23.899 per cent.; Coef. Cor., .5496 ± .0272.

TABLE XLII.

Correlation Table for Length and Breadth of 62 Dividing Specimens of Lot 2. (Descendants of *D;* See Table X., row 31.)

Length in Microns.

Breadth in Microns.	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	
40														1					1
44	1				2	2										1			6
48			1	1	1	2	1	3	3	2	2	1	1	1				1	20
52		1	1	2	2	7	3	3	5	1							1		26
56				1	2	1				1	2	1							8
60									1										1
	1	1	2	4	7	12	4	6	9	4	4	2	1	2	0	1	1	1	62

Length—Mean, 171.548 ± 1.188μ Breadth—Mean, 50.388 ± .308μ
St. Dev., 13.848 ± .840μ St. Dev., 3.584 ± .216μ
Coef. Var., 8.072 ± .492 Coef. Var., 7.111 ± .433

Mean Index, 29.583 per cent.; Coef. Cor., —.1136 ± .0840.

TABLE XLIII.

Correlation Table for Length and Breadth of Specimens in Early Stages of Fission: Constriction less than one-fourth Breadth. Lot 2. (See Table 10, row 30.)

Length in Microns.

Breadth in Microns.	144	148	152	156	160	164	168	172	176	180	
44	1				1	2					4
48			1	1	1	1	1	3	3	1	12
52		1	1	2	2	6	1	3	1	1	18
56				1	2	1				1	5
60									1		1
	1	1	2	4	6	10	2	6	5	3	40

Length—Mean, 165.200 ± .936μ Breadth—Mean, 50.700 ± .364μ
St. Dev., 8.788 ± .664μ St. Dev., 3.432 ± .260μ
Coef. Var., 5.320 ± .402 Coef. Var., 6.769 ± .513

Mean Index, 30.765 per cent.; Coef. Cor., .1048 ± .1055.

TABLE XLIV.

Correlation Table for Length and Breadth of Early Stages of Fisson, in Lot 3. (Depth of Constriction less than one-fourth Breadth.) (See Table X., row 24.)

Length in Microns.

Breadth in Microns.	152	156	160	164	168	172	176	180	184	188	192	
48			1									1
52												0
56	2				3				1			6
60		1	2			1						4
64	1		3	2		2		1		1		10
68	1		1	2		3	2		1		1	11
72				1	1	2						4
76			1	3			1					5
80								1				1
	4	1	8	8	4	8	3	2	2	1	1	42

Length—Mean, 167.620 ± .996μ Breadth—Mean, 65.716 ± .706μ
St. Dev., 9.564 ± .704μ St. Dev., 6.784 ± .499μ
Coef. Var., 5.706 ± .421 Coef. Var., 10.322 ± .768

Mean Index, 39.286 per cent.; Coef. Cor., .2215 ± .0999.

TABLE XLV.

Correlation Table for Length of Body and Depth of Constriction in 119 Dividing Specimens of the Aurelia form, Descended from c. (See Lot 4. Tables VIII. and X.)

Length in Microns.

Depth of Constriction, in Microns.	83.3	86.7	90.0	93.3	96.7	100.0	103.3	106.7	110.0	113.3	116.7	120.0	123.3	126.7	130.0	133.3	136.7	140.0	143.3	146.7	150.0	153.3	156.7	
3.3	1	1	1	5	3	10	11	6	9	3	1		2	1										54
6.7				1		4	3	3	1															12
10.0						1			1	2	2	1		1										8
13.3							1	3	2		2	2												10
16.7											1	2	1		3									7
20.0							1	1		2	1	4	2	1	1									13
23.3										1		1			3			1						6
26.7												1	1			2	1							5
30.0															1			1						2
33.3																					1		1	2
	1	1	6	3	15	16	13	13	8	7	11	6	3	8	2	1	2	0	0	1	0	1		119

Length—Mean, 111.541 ± .797μ Depth of Constriction, Mean, 10.504μ
St. Dev., 12.898 ± .564μ St. Dev. 8.431μ
Coef. Var., 11.563 ± .512

Coef. Cor., .7862 ± .0236. Increase in length with 10μ increase in depth of Constriction, 12.027μ.

TABLE XLVI.

Correlation Table for Length of Body and Depth of Constriction in 63 Dividing Specimens of the Aurelia form, Descended from c. (See Lot 5, Tables VIII. and X.)

Length in Microns.

Depth of Constriction in Microns.	93.3	96.7	100.	103.3	106.7	110.	113.3	116.7	120.	123.3	126.7	130.	133.3	136.7	140.	143.3	146.7	150.	153.3	
3.3	1		3		7		4	5	4		1									25
6.7					1		2	2	1	2	2									10
10.						1	2													3
13.3									2			1	1							4
16.7									1											1
20.											2									2
23.3										1	1									2
26.7												1				1		1		3
30.												2	1	1		1		1		6
33.3												1			2	1	1		1	6
36.7																			1	1
	1	0	3	0	8	1	8	7	8	3	6	5	2	1	2	3	1	2	2	63

TABLE XLVII.

Correlation Table for Length and Breadth of Dividing Specimens of Lot 4, in which the Depth of Constriction was Less than one-fourth the Breadth. (*Aurelia form, Descendants of c.*) (See Table X., row 33.)

Length in Microns.

Breadth in Microns.	83.3	86.7	90.	93.3	96.7	100.	103.3	106.7	110.	113.3	116.7	120.	123.3	126.7	
26.7	1														1
30.		1	1	2	1	3	2	1							11
33.3				2		11	6	2	2	1					24
36.7				2	2		5	4	4	2				1	20
40.							1	2	2		1		1		7
43.3									2				1		3
	1	1	1	6	3	14	14	9	10	3	1	0	2	1	66

Length—Mean, 103.737 ± .650μ Breadth—Mean, 34.850 ± .287μ
St. Dev., 7.823 ± .379μ St. Dev., 3.453 ± .203μ
Coef. Var., 7.541 ± .445 Coef. Var., 9.911 ± .587

Mean Index, 33.623 per cent.; Coef. Cor., .6502 ± .0479μ.

TABLE XLVIII.

Correlation Table for Length and Breadth of Dividing Specimens of Lot 5, in which the Depth of Constriction was Less than one-fourth the Breadth. (*Aurelia form, Descendants of c.*) (See Table X., row 36.)

Length in Microns.

Breadth in Microns.	93.3	96.7	100.	103.3	106.7	110.	113.3	116.7	120.	123.3	126.7	
33.3	1				2							3
36.7			1									1
40.			1		3	1		1				6
43.3			1				1	1	1			4
46.7					2		5	3	1	1	1	13
50.					1		2	2	1	1	2	9
53.3												0
56.7									2			2
	1	0	3	0	8	1	8	7	5	2	3	38

Length—Mean, 113.333 ± .850μ Breadth—Mean, 45.263 ± .597μ
St. Dev., 7.778 ± .603μ St. Dev., 5.463 ± .423μ
Coef. Var., 6.862 ± .533 Coef. Var., 12.071 ± .947

Mean Index, 39.903 per cent.; Coef. Cor., .6744 ± .0507.

TABLE XLIX.

Correlation Table for Length and Breadth of a Random Sample of Lot 4. (See Table 10. Aurelia form, Descendants of c. Many dividing.)

Breadth in Microns.	Length in Microns.																									
	73.3	76.7	80.	83.3	86.7	90.	93.3	96.7	100.	103.3	106.7	110.	113.3	116.7	120.	123.3	126.7	130.	133.3	136.7	140.	143.3	146.7	150.	153.3	156.7	160.	
20.					1																							1
23.3				1	1		1				1																	4
26.7	1			2	2	1		2	6	2	3	1	2					1										23
30.		1		2	2	1	5	6	5	6	7	6	6	1	1	2		1										52
33.3	1	1		1				3	4	3	2	5	7	7	6	2	4	2	3	2								53
36.7							1	1	2	2	3	3	2	7	5	5		2	4	1		3				1		42
40.				1					1		2			4	3	1	6	4	1	2	1	2		1		1		30
43.3												1			1		1	2			1	1	3					10
46.7									1								1				2			1	2	1	1	9
50.																						1						1
	2	2	0	7	6	2	7	12	19	13	18	16	17	19	16	10	12	12	8	5	4	7	3	2	2	3	1	225

Length—Mean, 114.163 ± .784μ Breadth—Mean, 34.207 ± .241μ
St. Dev., 17.443 ± .555μ St. Dev., 5.363 ± .171μ
Coef. Var., 15.279 ± .497 Coef. Var., 15.683 ± .511

Mean Index, 30.177 per cent.; Coef. Cor., .6757 ± .0244.

TABLE L.

Correlation Table for Length and Breadth of a Random Sample of Lot 5 (Table X.). *Aurelia form; Descendants of c. 24 Hours in a Fresh Hay Infusion.*

Breadth in Microns.	Length in Microns.																				
	86.7	90.	93.3	96.7	100.	103.3	106.7	110.	113.3	116.7	120.	123.3	126.7	130.	133.3	136.7	140.	143.3	146.7	
36.7				2	3	1	1													7
40.	1	1		3	1	3	3	1	1											14
43.3			1	2	3	1	6	2	2	3	2									22
46.7				1			1		5	5	1									13
50.							1		4	5	5	1	1		1			1		19
53.3							1			1	2	4	2	2	1					13
56.7												1	2	1		1	1			6
60.								1				2				1				4
63.3																		1		1
66.7																			1	1
	1	1	1	8	7	5	13	4	12	14	10	8	5	3	2	2	1	2	1	100

Length—Mean, 114.033 ± .820μ Breadth—Mean, 47.300 ± .437μ
St. Dev., 12.140 ± .580μ St. Dev., 6.490 ± .310μ
Coef. Var., 10.646 ± .513 Coef. Var., 13.720 ± .667

Mean Index, 41.455 per cent.; Coef. Cor., .8152 ± .0226.

TABLE LI.

Correlation Table for Length and Breadth of a Random Sample of the Culture from which came the Young of Lot 6, Table X., *after 24 hours in fresh hay infusion.* (See row 2, Table XVIII.)

Length in Microns.

Breadth in Microns.	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	
44		1																	1
48		2		1															3
52				3	2	1		2											8
56	1		2		3	2		1								1			10
60		1			1	1	3	1	4	1	1	1							14
64				1	3	2	1	5	1	4		1							18
68						1	4	4	2	2	4	1		1					19
72						2		3	2	1	2		3						13
76								2	2		1	1	2	1					9
80												1							1
84									2									1	3
88													1						1
	1	4	2	5	9	9	8	18	13	8	8	5	6	3	0	0	0	1	100

Length—Mean, 184.680 ± .848μ Breadth—Mean, 64.880 ± .580μ
St. Dev., 12.596 ± .600μ St. Dev., 8.624 ± .412μ
Coef. Var., 6.821 ± .327 Coef. Var., 13.292 ± .645

Mean Index or Ratio of Breadth to Length, 35.131 per cent.; Coef. Cor., .6469 ± .0392.

TABLE LII.

Correlation Table for Length and Breadth of Descendants of D, in Culture Fluid where Injurious Bacteria have Multiplied. June 25. (See row 5, Table XVIII.)

Length in Microns.

Breadth in Microns.	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	228	232	236	240	244	248	252	256	
36					1					1				1																	1
40					1				1	2	1	1	1	1		2		1													2
44	1				1			1	3	1	1	6			1	3	2	1	1	1											12
48				1		2	1	2	3	8	5	4	2	5	1	3		1	1												24
52			1		1					4	1		1	2	6	1	5	1	5	4	1	1	3	1	1						36
56		1					1		1		2	1		1	3	2		3	2	2	4	3		1							39
60														1			2		2	3	2		2	1		1		1		26
64														1		1	2		2	1	1	1	2	3	2						15
68																		1	1							1	1				4
72																	1								1				1		3
76																												1			1
80																															1
	1	0	1	0	3	1	4	1	6	8	14	15	6	5	11	15	10	11	7	13	10	8	5	7	7	4	2	1	1	1	178

Length—Mean, 201.888 ± 1.147μ Breadth—Mean, 56.112 ± .395μ
St. Dev., 22.680 ± .811μ St. Dev., 7.808 ± .279μ
Coef. Var., 11.233 ± .407 Coef. Var., 13.913 ± .507

Mean Index or Ratio of Breadth to Length, 27.850 per cent.; Coef. Cor., .6771 ± .0274.

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TABLE LIII.

Correlation Table for Length and Breadth of a Starving Culture of Descendants of D. Eleven days in small watch glass of hay infusion, not renewed. (See row 6, Table XVIII.)

Length in Microns.

Breadth in Microns.	128	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	
28		3				1	2										6
32	1		1	6	2	5	1	2									18
36	1		2	6	7	2	4	3			1			1			27
40	1	1	1	1	2	4	6	1	2	3	1	1					24
44				3	1	3	6		2	1	2					1	19
48							1	1	2								4
52									1			1					2
	3	4	4	16	12	15	20	7	7	4	4	2	0	1	0	1	100

Length—Mean, 149.360 ± .736μ Breadth—Mean, 38.080 ± .356μ
St. Dev., 10.896 ± .520μ St. Dev., 5.288 ± .252μ
Coef. Var., 7.296 ± .350 Coef. Var., 13.881 ± .675

Mean Index or Ratio of Breadth to Length, 25.515 per cent.; Coef. Cor., .4481 ± .0539.

TABLE LIV.

Correlation Table for Length and Breadth of Descendants of D, in a rather Ill-fed Culture. September 15. (See row 13, Table XVIII.)

Length in Microns.

Breadth in Microns.	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	228	232	
40							2	2	2	1										7
44				1		1	1	3		1	2		2			1			1	13
48	1					1	1	2	2	7	6	1	5	1	2	1				30
52					1	1	2	3	3	3		2	4	3	3	3	4	3		35
56							1	2	1		1	2		1		1	1	2	1	13
60																	1		1	2
	1	0	0	1	1	3	7	12	8	12	9	5	11	5	5	6	6	5	3	100

Length—Mean, 202.280 ± 1.031μ Breadth—Mean, 49.600 ± .298μ
St. Dev., 15.284 ± .729μ St. Dev., 4.412 ± .210μ
Coef. Var., 7.556 ± .362 Coef. Var., 8.896 ± .428

Mean Ratio of Breadth to Length, 24.593 per cent.; Coef. Cor.. .4085 ± .0562.

TABLE LV.

Correlation Table for Length and Breadth of the Same Lot Shown in Table LIV., but after 48 hours in fresh hay infusion. September 15.
(See row 14, Table XVIII.)

Length in Microns.

Breadth in Microns.	124	128	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	
44								1																	1
48												1													1
52					1	1		1	1		1	2	1		2										10
56								1	2	2	3		1		1		1								10
60								1	1	3	3	2	3	4	2	3	2		1						25
64			1						3		1	1	1		1	1	4	1							14
68	1											3		3	4	4	1	1	2					1	20
72											1	1		1		1	3	4	2	1	1				15
76																	1	1		1					3
80																		1							1
	1	0	1	0	1	1	0	3	7	5	9	10	6	8	10	9	12	8	5	2	1	0	0	1	100

Length—Mean, 175.320 ± 1.060μ Breadth—Mean, 63.160 ± .472μ
St. Dev., 15.708 ± .749μ St. Dev., 7.000 ± .334μ
Coef. Var., 8.959 ± .431 Coef. Var., 11.083 ± .535

Mean Ratio of Breadth to Length, 36.123 per cent.; Coef. Cor., .5376 ± .0489.

TABLE LVI.

Correlation Table for Length and Breadth of Descendants of c. August 9.
(See row 17, Table XVIII.)

Length in Microns.

Breadth in Microns.	100	103.3	106.7	110.	113.3	116.7	120.	123.3	126.7	130.	133.3	136.7	140.	143.3	146.7	150.	153.3	156.7	160.	
23.3	2	1	2		1	1		1	1											9
26.7	1		1	5	1	3		1				1		1						14
30.			2	1	3	1	4			1	1									13
33.3				2	2	3	2	2	1	4	3	2								21
36.7					2	1	4	4	2	1	3		1	3	1					22
40.						1	2	1		5	1				2					12
43.3									1	2		1	1		1				1	7
46.7												1								1
50.													1							1
	3	1	5	8	9	10	12	9	5	13	8	5	3	4	4	0	0	0	1	100

Length—Mean, 123.666 ± .813μ Breadth—Mean, 33.600 ± .400μ
St. Dev., 12.040 ± .573μ St. Dev., 5.917 ± .283μ
Coef. Var., 9.736 ± .469 Coef. Var., 17.608 ± .865

Mean Ratio of Breadth to Length, 27.136 per cent.; Coef. Cor., .6528 ± .0410.

TABLE LVII.

Correlation Table for Length and Breadth of a Sample of the Non-Conjugants of a Conjugating Culture of Descendants of the Individual c. Flourishing culture in a large vessel. September 25, 1907. (See row 21, Table XVIII.)

Length in Microns.

Breadth in Microns.	124	128	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	
16				1																	1
20			1																		1
24		2	1	1	2																6
28	2		4	4	1	5	1	1	1												19
32		1	3	2	1	3	3	3	3		2	1		1			1				24
36			1	5	5	8	5	2	7	2	5	1		1							42
40					2	3	2	9	5	7	3	1	5	4	2	3	1			1	48
44							2	2	1	2	4		2	5	1	3		2		1	25
48							1	1	2		1	4		2	2	3	3	2	1		22
52												1		1	1	3		1	2		9
56																		2		1	1
60																					2
	2	3	10	13	11	19	14	18	19	11	15	8	7	14	6	12	5	7	3	3	200

Length—Mean, 158.800 ± .877μ Breadth—Mean, 38.560 ± .353μ
St. Dev., 18.384 ± .620μ St. Dev., 7.396 ± .249μ
Coef. Var., 11.578 ± .396 Coef. Var., 19.176 ± .670

Mean Ratio of Breadth to Length, 24.244 per cent.; Coef. Cor., .7135 ± .0234.

TABLE LVIII.

Correlation Table for Length and Breadth of Descendants of c, Five Days after Cessation of Conjugation. Food getting scarce. September 30, 1907. (See row 22, Table XVIII.)

Length in Microns.

Breadth in Microns.	100	104	108	112	116	120	124	128	132	136	140	144	148	152	
20		1			1										2
24	1			1				2							4
28			4	5	1		3			1					14
32			2	3	4	3	1	2	2	2	1				20
36				1	1	1	2	2	5	4		1	2		19
40						1	1	1	3	5	10	6	2	2	31
44											4	2	1		7
48										1	1		1		3
	1	1	6	10	7	5	7	7	10	13	16	9	6	2	100

Length—Mean, 129.640 ± .867μ Breadth—Mean, 35.440 ± .400μ
St. Dev., 12.848 ± .613μ St. Dev., 5.928 ± .283μ
Coef. Var., 9.911 ± .477 Coef. Var., 16.730 ± .820

Mean Ratio of Breadth to Length, 27.262 per cent.; Coef. Cor., .7576 ± .0287.

TABLE LIX.

Correlation Table for Length and Breadth in a Large, Old Culture of Descendants of c, January 23, 1908. (See row 23, Table XVIII.)

Length in Microns.

Breadth in Microns.	100	104	108	112	116	120	124	128	132	136	140	144	148	152	156	160	164	168	172	176	
32						2															2
36				1	3	1															5
40					1	1		1	1	2		1									7
44							2	2	3	1	1										9
48	1					1		1	2	4	2	7		1							19
52									1	1	2	1	3	1		1					10
56									1	1	2	1	1	5		2	1				14
60												2	2	1	1	3	1				10
64											1	1	1	1		1	2	1			8
68															1		2		3		6
72																	1	2	1		4
76															1	1			2		4
80																					0
84																		1		1	2
	1	0	0	1	4	5	2	4	8	9	8	13	7	9	3	8	7	4	6	1	100

Length—Mean, 144.880 ± 1.097μ Breadth—Mean, 54.160 ± .765μ
St. Dev., 16.264 ± .776μ St. Dev., 11.346 ± .541μ
Coef. Var., 11.224 ± .542 Coef. Var., 20.948 ± 1.042

Mean Ratio of Breadth to Length, 37.106 per cent.; Coef. Cor., .8500 ± .0187.

TABLE LX.

Correlation Table for Length and Breadth of Descendants of c. Same Culture shown in Table LIX, but cultivated in small watch glass, January 30 to February 15, 1908. (See row 27, Table XVIII.)

Length in Microns.

Breadth in Microns.	76	80	84	88	92	96	100	104	108	112	116	120	
16			1										1
20	1			6	2	3	1						13
24			2		6	11	6	3	2				30
28					3	1	11	11	11	1	1		39
32							3	5		4	1		13
36									1	2		1	4
	1	0	3	6	11	15	21	19	14	7	2	1	100

Length—Mean, 100.320 ± .528μ Breadth—Mean, 26.480 ± .266μ
St. Dev., 7.828 ± .373μ St. Dev., 3.944 ± .188μ
Coef. Var., 7.804 ± .374 Coef. Var., 14.895 ± .753

Mean Ratio of Breadth to Length, 26.321; Coef. Cor., .7671 ± .0278.

TABLE LXI.

Correlation Table for Length and Breadth of a Random Sample of the "Wild" Conjugating Culture M, January 29, 1908. 200 Non-conjugants, 38 Conjugants.

Length in Microns.

Breadth in Microns.	132	136	140	144	148	152	156	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	228	232	236	24	
28									1																				1
32				1									2																3
36		1				1	3		3		1	1	1																11
40					2		2	2	7	4	4	5	1	2		1	1												31
44						1	2	1	5	6	7	5	4	1	2	6	2	1	2	1			1						47
48	1				1	1		3	1	4	5	5	6	2	6	7	1	5	2	1		1							52
52		1						1	1	5	2	4	3	1	2	5	6	1	4	3					1				40
56													1	3	2	4	1	1	1		3	2							18
60												2					2												4
64																2	2	1	1	2			1					1	10
68										1		2			3		2	1			1				1				11
72																1							1						2
76															2			1		1									4
80																	1				1								2
84																													0
88																		1					1						2
	1	2	0	1	3	3	7	7	18	20	19	24	18	9	17	26	18	12	10	8	5	3	4	0	2	0	0	1	238

TABLE LXII.

Correlation Table for Length and Breadth of Dividing Specimens of Lot 1 (Table X.), in which Lengthening had begun. (Constriction more than 4 microns deep.)

Length in Microns.

Breadth in Microns.	160	164	168	172	176	180	184	188	192	196	200	204	208	212	216	220	224	
40					2						1		1				1	5
44	2	1		3	2			2	5	2	4	2	2	3	1		1	30
48		2	10	9	5	7	8	8	8	4		3	2		3	2		71
52		2	2	10	10	4	12	2	2	4	1	1			1			51
56					3	4	2		1	1	3	3	1					18
60					1	1		3		1								6
64																		0
68															1			1
	2	5	12	22	23	16	22	15	16	12	9	9	6	3	6	2	2	182

Length—Mean, 186.066 ± .710μ Breadth—Mean, 49.540 ± .215μ

St. Dev., 14.208 ± .502μ St. Dev., 4.296 ± .152μ

Coef. Var., 7.636 ± .271 Coef. Var., 8.671 ± .309

Mean Ratio of Breadth to Length, 26.796 per cent.; Coef. Cor., —.0938 ± .0496.

TABLE LXIII.

Correlation Table for Length and Breadth of Dividing Specimens of the Aurelia Form (Descendants of c), in which Lengthening had begun.

(See Lot 4, Tables VIII. and X.)

Length in Microns.

Breadth in Microns.	100.	103.3	106.7	110.	113.3	116.7	120.	123.3	126.7	130.	133.3	136.7	140.	143.3	146.7	150.	153.3	156.7	
26.7			1		1					1									3
30.			1	1	1	1		2		2	1		1						10
33.3	1	1	2	2	2	2	4	1		1	1	1							18
36.7		1				3	5			2									11
40.					1		2	1		2	1					1		1	9
43.3									1										1
46.7													1						1
	1	2	4	3	5	6	11	4	1	8	3	1	2	0	0	1	0	1	53

Length—Mean, 121.383 ± 1.053μ Breadth—Mean, 34.590 ± .383μ
St. Dev., 11.367 ± .743μ St. Dev., 4.147 ± .273μ
Coef. Var., 9.365 ± .613 Coef. Var., 11.989 ± .797

Mean Ratio of Breadth to Length, 28.648 per cent.; Coef. Cor., .3100 ± .0837.

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ON THE MORPHOLOGY OF THE EXCRETORY ORGANS OF METAZOA: A CRITICAL REVIEW.

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(*Read April 24, 1908.*)

The desire to acquaint myself with modern ideas as to the homologies of the excretory organs has led to the present review. These organs constitute a chapter in comparative anatomy that is one of the most compendious and intricate of all. Their relations are so broad and manifold that no morphologist can go far without touching upon them, and one need not wonder at this because their function is above all others necessary to the continuance of the life of the individual.

Among those who have contributed largely to this subject are Balfour, Bergh, Bürger, Cuénot, Eisig, Goodrich, Hatschek, Lang, Eduard Meyer, Sedgwick and Vejdovský, but the bibliography shows how many well-known investigators have added to our knowledge. There is a wealth of accumulated facts that have never been treated critically in their entirety, and on that account the present bringing together of them may be of help to future students.

This memoir is divided into two portions: (*A*) a descriptive one, in which the groups of Metazoa and their particular excretory organs are treated in succession; and (*B*) a comparative one, in which all the excretory organs are reduced to certain types, and then the homologies of these discussed. It is in this second part that a standpoint is reached different, so far as I know, from previous ones, one that I hope puts the facts in a clearer light.

A. DESCRIPTIVE.

The following is a brief summary of our knowledge of the general structure and embryogeny of special excretory organs considered separately for each group. Histological details are not

entered upon. I have endeavored to consult all the more important literature up to 1907, but at the same time to refer in the citations to only the more comprehensive accounts; the literature references therefore do not by any means represent complete bibliographies, but refer the reader to the more important memoirs.

The Orthonectida, Dicyemida, Cnidaria and Porifera lack special excretory organs; and such structures are still unknown for *Cephalodiscus, Rhabdopleura,* the Chaetosomatidæ, Desmoscolicidæ, and Pentastomida.

1. Ctenophora.

Here there are short, presumably entoblastic, canals that connect the aboral canal (funnel canal) of the gastro-vascular cavity with the aboral surface of the body; there may be two or four of these openings; these discharge injected carmine, while there is no evidence that water is taken in through them (Chun, 1880).

2. Plathelminthes.

These possess branching, tubular organs whose finest branches (capillaries) have intracellular cavities and terminate in closed flame cells, the latter being very small and numerous. Nothing is known as to their embryonic origin, except the one observation of Lang (1884) that in Polyclades a pair of solid ingrowths of the ectoblast seems to represent their beginnings. The main structural variations are with regard to the number, ramification and degree of anastomosis of the main canals, and the number and position of nephridiopores and excretory canals.

(1) *Turbellaria.*

Polycladidea.—Discovered by Max Schultze (1854) these organs have received subsequent description only by Lang (1884), who found that the terminal flames are unicellular and who could trace the supposed excretory canals of *Thysanozoon* to the dorsum, but could not find their openings there. Accordingly, a complete knowledge of their structure is still a desideratum. I have not been able to find them on sectioned material.

Rhabdocœlida.—Here they appear to be absent only in the

Acœla. Three chief types have been distinguished (v. Graff, 1882): a single main canal with a single nephridiopore (*Stenostoma*); a pair of main canals with independent nephridiopores, and a pair of main canals with a common nephridiopore. In *Bothrioplana* (Vejdovský, 1895) there are two pores different in structure, one at the middle and the other at the anterior end of the body; into the former open two main canals, each of the latter divides into an anterior and a posterior branch, and these anterior branches connect also with the anterior nephridiopore. In the Eumesostomina (Luther, 1904) the main canals open independently either on the surface of the body, or into the mouth, or into the genital atrium (all these being ectoblastic), and besides the terminal flame cells there are other flames (without nuclei) interpolated in the course of the canals. In these forms there is never more than one pair of main canals, or more than two nephridopores.

Tricladidea.—In *Planaria* but more specially *Gunda* Lang (1881) described two main ducts on each side of the body, each bearing numerous capillaries ending in flame cells; there are anastomoses between the former but not between the latter; from each main duct proceeds a series of excretory ducts each of which opens dorsally by a small contractile vesicle. And Böhmig (1906) adds to this account of *Gunda* by the discovery of four pairs of main canals, and of ventral as well as dorsal nephridiopores. In *Dendrocœlum* Ijima (1885) found similar relations, though he held there to be but one main canal on each side; while Wilhelmi (1906) found two of them with a segmental arrangement of eight pairs of excretory ducts, and (in opposition to the earlier observations of Chichkoff) no openings into the pharynx. The Tricladidea differ from the Rhabdocœlida in the presence of numerous serial excretory ducts.

(2) *Trematoda.*

The chief characteristic of the excretory organs is their dendritic branching and their degree of anastomosis. In the Monogenea there are usually paired nephridiopores (in *Gyrodactylus* a single one) placed in most cases at the anterior end but sometimes at the posterior. The excretory vesicle of the Digenea is at the posterior

end, terminal or dorsal, and into it open usually two but sometimes four or even six main canals (Braun, 1893). In the larva (miracidium) of *Distomum* there is a single large flame cell on each side of the body with a capillary opening on the surface (Coe, 1896). Bugge (1902) has shown that each flame cell and its capillary "develop out of one cell and are to be compared with a unicellular gland," a practical confirmation of Lang's (1884) suggestion.

(3) *Temnocephaleæ.*

The excretory system of these curious forms has been made known particularly by Weber (1889). There is a pair of separated dorsal nephridiopores, each communicating with main canals that branch and anastomose with those of the opposite side, so that the general arrangement is like that of the Trematoda.

(4) *Cestoda.*

Here the main canals have no dendritic branching but frequent anastomoses, so that quite generally each proglottid has one or two pairs of transverse canals connecting the main lateral ones; the main lateral canals open by a common contractile vesicle at the posterior end of the ripest proglottid (Pintner, 1896). In the most detailed contribution on the subject (Bugge, 1902) muscle fibrils of the main canals are described and also valves within them (the latter discovered by Köhler in 1894); in the cysticercus stage foramina secondaria were found connecting the main canals with the surface of the body. Bugge uses the term "Wimperflamme" to include the "Terminalzelle" ("Geisselzelle, Deckzelle"), with the "Wimper" and "Trichter" and "Capillare." He traced such Wimperflammen as outgrowths from the walls of the main canals: a cell of the latter projects outwards then divides into a group of four; of these four one forms three Trichter and the capillary (the cavities of these parts being intracellular), while each of the three others becomes a flame cell with a ciliary flame.

Anatomically considered there are two main kinds of excretory organs in the Platyhelminthes: (1) with numerous serial excretory canals, found only in the Tricladidea; and (2) with only one or

two excretory canals, found in all the others (though the relations are not yet known for the Polyclades).

3. Nemertini.

From the comprehensive treatment given by Bürger (1895), based largely upon his own researches, it follows that the excretory organs are as a rule in the form of two main canals parallel with the lateral blood vessels and not communicating together; each opens to the exterior of the body by one, or more rarely by a series of several (up to about forty), excretory ducts; the main canals are usually restricted to the region of the stomach, but in some genera they extend the length of the body. From them proceed delicate capillaries that terminate blindly in multicellular "Endkölbchen"; the latter may project into the walls of blood vessels, but (contrary to the earlier opinion of Oudemans) there is no open communication of any portion of the nephridia with these vessels or other internal cavities. In the freshwater *Stichostemma* I showed (1897) that an unusual condition obtains, in that in the adult instead of a single canal on each side there is a series of them, some with and some without excretory canals; and then Böhmig (1898) demonstrated that the latter are produced by a secondary segmentation of originally continuous ducts.[1] Punnett (1900) and Coe (1906) found in *Tæniosoma* besides excretory pores opening on the surface of the body others that connect with the œsophagus; the latter are clearly embryonic ducts persisting in the adult.

The larvæ do not possess special excretory organs. The definitive ones arise, according to Bürger, as a pair of hollow evaginations of the ectoblastic stomodæum of the larva, soon abstrict from the œsophagus and then open into the amniotic cavity at a ventral point near the mouth, a position quite different from that of the adult excretory pores. The origin of the latter is not known, and

[1] I had described the terminal bulbs of this genus as closed from the capillaries, with an internal cuticular lining but no flame, while Böhmig found them essentially as described by Bürger except that each consists of usually not more than two cells. I have recently had opportunity to examine living material and to compare it with my former sections, and find I had overlooked the true flame cells and that Böhmig had described them correctly. Each terminal bulb consists of from one to five cells.

Bürger suggests they may either be secondary invaginations of the epidermis, " or the nephridium itself must break a new way through the body wall. Judging from the adult animal the first alternative must be the case."

4. Gastrotricha.

There is a single pair of much convoluted tubules, lateral from the intestine, opening near each other on the ventral surface without excretory vesicles. Each ends internally with a single closed bulb, but it is not determined whether it contains a single flagellum or a row of cilia (Zelinka, 1889).

5. Rotatoria.

The excretory organs have been most carefully described for the Philodinidæ (Zelinka, 1886, 1888, 1891, Plate, 1889), Flosculariidæ (Montgomery, 1903, Gast, 1900), Melicertidæ (Hlava, 1904, 1905), Atrochidæ (Wierzejski, 1893) and Asplanchnidæ (Hudson and Gosse, 1886, Rousselet, 1891, Weber, 1898). There is always a right and left main canal; the flame cells may be directly attached to these (most Philodinidæ), but more usually are placed at the ends of capillaries, branches of a main capillary that open into the main canal at one or two points. The number of flame cells on eash side of the body is small, usually from three to six, and in that case they are relatively large; but in the Asplanchnidæ there are some fifty of them on each side sessile on a main capillary. Their great number here may be due to the large size of these species. The main canals unite posteriorly into a short unpaired duct that opens into the cloaca; and anteriorly they are usually connected by a transverse commissure (absent in some Philodinidæ). The main canals have an intracellular cavity, are composed of a few cells and are usually without cilia; terminal flame and capillary is a single cell, the termination of which is entirely closed from the body cavity and contains an internal flame of cilia and (in *Asplanchna*) has a couple of long flagella on the outer surface.

The early development of these structures has not been determined (Zelinka, 1891).

6. Endoprocta.

Joliet (1880) described for *Pedicellina* and *Loxosoma* a pair of short ciliated canals with a common nephridiopore, and with their inner ends open to the body cavity. Prouho (1890) leaves the question unsettled whether these ends are open or closed. All other observers describe the inner termination of each canal as closed by a flame cell: so Foettinger (1887) and Ehlers (1890) for *Pedicellina,* Harmer (1885, *Loxosoma*), and Davenport (1893, *Urnatella*). The cavity of these canals is intracellular, and only in *Loxosoma* are there paired nephridiopores.

Besides this "Chief excretory apparatus" Davenport found in the stalk of *Urnatella* "elongated spaces terminating blindly at one end in structures which must be regarded as flame cells . . . I have not, however, been able in any instance to trace an individual tubule to any considerable distance, or until it opens into any other organ."

Accordingly, all Endoprocta seem to have a pair of nephridia internally closed that do not serve as genital ducts, and in one genus flame cells seem to occur in the stalk.

In regard to their development, Hatschek (1877) found in the full-formed larva of *Pedicellina* a pair of ciliated canals like those of the adult, but did not determine either their structure or origin. It would seem probable that this excretory organ persists in the adult.

7. Rhodope.

For this curious form that has been variously related to the Turbellaria and the opisthobranch mollusks, Böhmig (1893) described a nephridiopore on the right side just anterior to the anus, into which opens a "Urinkammer"; into the latter discharge ramified ducts, and to each of these are attached about forty flame-bearing terminal organs, each completely closed from the body cavity and consisting of from four to eight cells. Nothing is known of the development.

8. Acanthocephala.

The excretory organs of this group are known only from the observations of Kaiser (1892, 1893). They occur only in the large *Echinorhynchus gigas* and seem to be absent in the smaller

species (I also have looked for them in vain in a number of American species). In the female there is a pair of them discharging into the oviduct; each is a broad spade-shaped organ composed of three cells, the free end branched dendritically, each finest subdivision of which terminates in a perforated membrane bearing on the luminal side a tuft of long cilia; there are about five to six hundred of these terminal flames to each nephridium, though the whole organ it will be recollected is composed of only three cells. The Acanthocephala are specially characterized by the small number but great degree of specialization of their cells. In the male the nephridia open into the ductus ejaculatorius, and are similar to those of the female save that the terminal flames are less numerous. Kaiser supposes that in the smaller species lacking these organs the oviduct is excretory, since in them the uterus bell is open to the body cavity.

They arise conjointly with the genital ducts from the ectoblast.

9. Chætognatha.

No excretory organs were found by Hertwig (1880), while Grassi (1883) suggests that a pair of small glands opening at the junction of the head and prepuce may be urinary.

The genital ducts are not comparable with nephridia because they do not develop until maturity, and because the vasa deferentia are ectoblastic and the oviducts are outgrowths of the ovaries (Doncaster, 1902).

10. Kinorhyncha.

The genus *Echinoderes* exhibits one pair of short, pyriform canals, ciliated throughout, with enlarged closed inner ends, that open separately and dorso-laterally (Reinhard, 1887).

11. Nematoda.

As first made known by Anton Schneider (1866) and confirmed by most subsequent writers there is usually an excretory duct in each lateral line (though one may be wanting) that extend from the posterior region of the body to the œsophagus, where they converge and open by a single median nephridiopore. The inner ends

of these canals are closed, and each is lined by a cuticula. Four types of these have been distinguished according to their form and position of the nephridiopore (Jägerskiöld, 1898). A more careful description has been furnished by Goldschmidt (1906) for *Ascaris lumbricoides,* who found that the whole apparatus is composed of but two cells, with a single nucleus for both main canals and one for the anterior unpaired duct. Goldschmidt further considers these canals to be simply for discharge, and that a peculiar solid tissue of the lateral lines is the true secretory portion; these glandular masses are multinuclear and do not touch the walls of the canals, but fine pores appear to extend towards them from the lumina of the canals. In his own words: "The excretory system of *Ascaris* . . . consists of the excretory gland proper (analogous to a kidney) that lies within the lateral lines, and of the discharge duct (analogous to a ureter) that consists of two horseshoe-shaped limbs composed of a single cell and of an unpaired terminal portion represented by one cell."

Little is known of the development of these canals. They lie within the lateral lines, and Zur Strassen (1892) has shown that the latter are mesoblastic. Conte (1902) found the excretory apparatus to arise from a single mesoblast cell that becomes secondarily placed in the lateral line.

12. Gordiacea.

For this group specific excretory organs are still unknown, though it has received much study. Vejdovský (1886, 1894) has interpreted the peri-intestinal cavity as excretory, but this has no opening to the exterior; and he has suggested that the oviducts and vasa deferentia are modified nephridia,—a conclusion drawn from his idea that the Gordiacea are degenerate annelids, a standpoint that has been combated by me (1903*a*). In late embryonic stages he found a "braune Drüse" opening into the intestine near the mouth; this is not found in the adult, unless the problematical supra-intestinal orgon described by me for *Paragordius* may be an excretory organ conveying fluids from the peri-intestinal space to the intestine. It is probable that excretion must take place through

either the genital ducts or the intestine, since the thick cuticula on the surface of the body is hardly permeable.

The gland of the larva construed by Villot (1874) as an excretory organ has been considered by me (1904) to be rather a poison gland; I have shown that its body develops as an abstriction of the entoblast, and that its duct opens at the base of the proboscideal stilets; it is completely closed from the body cavity and does not possess cilia.[2]

13. Ectoprocta.

For the Phylactolæmata the fullest description is that of Cori (1893, *Cristatella*), according to whom there is a nephridium just above the anus, between the body wall and the peritoneum, consisting of two ciliated nephrostomes opening into the cœlom, connecting with an enlarged sac that has a single nephridiopore near the cerebral ganglion. He proved experimentally that lymphocytes ingest waste particles, and then are discharged by this organ.

In the Gymnolæmata there is in some species an organ discovered by Hincks (1880), and more fully described by Prouho (1892) who names it the "organe intertentaculaire"; this occurs only in sexual individuals, is primarily a genital duct, and is a ciliated canal with an inner nephrostome. In most Gymnolæmata special excretory organs are absent (Ostroumoff, 1886, Harmer, 1891). Harmer concludes from injection experiments that excretion is performed "partly by the cells which I have described as leucocytes, partly by the walls of the alimentary canal, and partly by the funicular tissue," while he and Ostroumoff have proved that the formation of the "brown body" and the death of the polypid is due to an accumulation of waste substances especially in the intestine.

The larvæ lack excretory organs, and the development of those of the adult has not been described.

14. Sipunculida.

There are as a rule two "excretory tubes," but within the same genus either two or one may occur. In most cases each of these has

[2] In the marine *Nectonema*, that shows some similarity to the diplobiotic Gordiacea, excretory organs are unknown.

a nephridiopore on the ventral surface of the body, and a ciliated nephrostome placed at the inner end of the tube or else near the external opening. But in *Sternaspis* Goodrich (1897) found no nephridiopores, and in an immature individual of *Phascolosoma proki* Sluiter (1882*b*) found no nephrostomes. In all cases these serve as genital ducts. Metalnikoff (1900), in the most detailed memoir, concludes that the nephrostome cannot serve excretion but acts merely to swallow the germ cells, while excretion must be accomplished by osmosis through the wall of the organ that is lined by cells resembling the chloragogue of annelids. Goodrich holds these are not true nephridia, but "peritoneal funnels peculiarly modified."

The embryological data are conflicting. In *Phascolosoma* Gerould (1906) found no excretory organs in the trochophore, and in the "larva" (that succeeds the trochophore) the definitive nephridia arise as solid ectoblastic ingrowths ("a pair of ingrowths, probably of ectoderm"), to which are added funnels of mesoblastic origin. In *Sipunculus* Hatschek (1883) described a pair of "Nierenzellen" in the mesoblast of the embryo; each of these divides into four cells which acquire an intracellular cavity, then one end of each cell cord becomes attached to the ectoblast while the other opens into the cœlom. Gerould's account is the much more detailed and thorough, and renders it probable that both ectoblast and mesoblast enter into these nephridia. The trochophore lacks nephridia.

15. Priapulida.

For these animals we have only the brief description of Schauinsland (1886), unaccompanied by figures. From each side of the posterior end there is said to invaginate a pair of ectoblastic tubes. Then a series of short excretory tubules grow out from the walls of these; the "Endorgane" are multicellular, closed from the body cavity, each cell with a long flagellum. Still later other folds evaginate from the walls of the main ducts, and their cells become the reproductive elements. According to this description this would be a unique ectoblastic organ, not unlike that of the Plathelminthes, that proliferates germ cells.

16. PHORONIDEA.

In the adult just behind the transverse septum Cori (1890) found a pair of ciliated canals with open nephrostomes, and determined that their function is both genital and urinary. In *Phoronis australis* Benham (1889) found that each tube has two nephrostomes, and a similar relation was discovered by Cowles (1905).

There is quite general agreement that the larval nephridia are ectoblastic (Ikeda, 1901, Longchamps, 1902, Shearer, 1906, Cowles, 1905); from a nephridial pit at the posterior end grow out the two canals whose cavity is intercellular. The observers already cited together with Caldwell (1882) and Goodrich (1903), in contradiction to Masterman (1897), agree further that the nephridia of the actinotrocha are closed at their inner ends from the blastocoel in which they lie; and Shearer, who gives the most complete account of the development of these structures, shows that their inner ends are closed by a group of solenocytes that represent outgrowths from the tubes. Longchamps states that these larval organs persist into the adult; this is assumed by Shearer who decides that these canals "acquire openings into the cœlom by means of ciliated funnels of unknown origin"; while Ikeda concludes: "We may assume that the formation of the infraseptal nephridial funnels of the adult is due to secondary outgrowths of the infraseptal portion of the atrophied, larval nephridial canals." The only point not fully decided is that of the origin of the funnels.

17. BRACHIOPODA.

According to the monographs of Van Bemmelen (1883), Blochmann (1900) and Morse (1902) there is usually one pair of supposed excretory organs, with nephrostomes and nephridiopores, that serve as genital ducts; in *Hemithyris* and *Rhynchonella* there are two pairs.

Nothing is known of their development, and there appear to be no larval nephridia.

18. ECHINODERMATA.

Crinoidea.—Special excretory structures are unknown.

Echinoidea.—The axial organ (ovoid gland) has been consid-

ered an excretory organ (Hamann, 1887, Sarasin, 1888, Ludwig, 1889) and proved to be so by carmine injection (Kowalevsky, 1889), while to it has also been ascribed the function of producing cœlomic cells (Leipoldt, 1893). It is a slender axial sac, the oral end of which ends blindly, opening by a delicate canal under the madreporite close to the stone canal; it is composed of a meshwork of trabeculæ of connective tissue, covered internally by an epithelium, in the meshes of which lie amœboid cells (Ludwig). Hamann described its cavity as communicating with blood lacunæ and the Sarasins as connecting with the body cavity by nephrostomes, but these results have not been confirmed and the bulk of evidence points to its being closed from other body cavities.

Ophiuroidea.—Here both respiration and excretion take place osmotically through the walls of the genital bursæ (Cuénot, 1888).

Asteroidea.—By injection Kowalevsky (1889) found that the bodies of Tiedemann are the excretory organs of the ambulacral system. Cuénot (1901) distinguished (1) amœbocytes, floating cells in the cœlom, blood vessels and ambulacral system, that are first phagocytic, and when they become laden with excretory products leave the organism by passing through the walls of the gill sacs; and (2) nephrocytes. Of the latter he distinguished: those that take up indigo (epithelium of the intestinal cæca), and those that ingest carmine (peritoneum, epithelia of perihæmal spaces and ambulacral vessels, inner cells of septal organs).

Holothurioidea.—In the Synaptids the "ciliated funnels" have been proved to collect waste products, by their ciliary action and agglutinating secretion; such products and amœbocytes loaded with them become caught in these organs, and ultimately make their way through the solid tissues to become deposited beneath the skin (Schultz, 1895, Cuénot, 1902). These funnels are generally arranged in rows on either side of the mesenteric radix, and project into the cœlom either separately or in groups. Each is a somewhat spoon-shaped, flattened prominence, with a concave ciliated surface, attached to the wall of the cœlom by a slender stalk, both plate and stalk being composed of solid connective tissue covered by peritoneum. Thus they are really not funnels at all, but solid projections into the body cavity, and cannot in any way be compared

with the peritoneal funnels (peritoneal evaginations) of other forms. In the Pedata the respiratory trees have been considered as in part excretory (Schultz, 1895); and the organs of Cuvier, tubes that also open into the cloaca behind the preceding, have been regarded as excretory by Hérouard (1893), but it is proven that these are rather eversible defensive structures (Minchin, 1892, Russo, 1889).

The ambulacral system of the echinoderms seems to mainly subserve locomotion, respiration and nutrition; but the bodies of Tiedemann, as mentioned above, that occur in it are excretory, and the Polian vesicle in holothurians may contain an "irregular non-living mass of brown spherules" which may be waste substances derived from the brown wandering cells occurring elsewhere in this system (Gerould, 1896).

The larvæ lack nephridia, and there appear to be no organs in this group comparable with excretory organs in others. The only representatives of peritoneal funnels are ciliated evaginations from the embryonic hydrocœl that join secondarily with ectoblastic invaginations; there is usually only one of these and it persists as the stone canal, but there may be two; Field (1892) compared the enterocœls with nephridia that have secondarily come into the service of locomotion.

There is little known of the development of the genital organs of Holothurioids. In Asteroids they have been described as coming from a solid mesenchyme mass that invaginates the peritoneum; only in Echinoids is the gonad stated to be peritoneal, a proliferation of cells of the left posterior enterocoel. Accordingly, there is no evidence that the gonads or their ducts stand in relation to nephridia.

15. Tunicata.

Special organs of excretion fail in the Appendiculariæ (Seeliger, 1893), and I have not found them described for the Doliolidæ. For other forms Dahlgrün (1901) has distinguished the following kinds: (1) Scattered excretory cells, in the visceral region (in *Botryllus, Botrylloides, Polycyclus, Ciona, Salpa*); (2) vesicles, rather numerous in the connective tissue, each with a wall formed of prismatic cells and with fluid or solid contents (*Ascidiella,*

Ascidia); (3) sacs, less numerous, on both sides of the body below the mantle, with walls of cubical cells (*Cynthia, Microcosmus*); and (4) renal organs, a single voluminous sac on the right side of the body with epithelial wall (*Molgula*). Todaro (1902*a*, *b*) described them for the Salpidæ as hollow vesicles in the number of three pairs, to which waste products are carried by the blood corpuscles.

Thus in the majority of Tunicates they are vesicles without ducts placed in the mesenchyme. Van Beneden and Julin (1886) found them to be derived from mesenchyme, and concluded that this embryonic tissue is a modification of what was ancestrally enterocœlic mesoblast; Conklin (1905), however, has shown that all the mesoblast is peristomial, consequently the tissue from which these organs develop may be mesectoblast.

The genital ducts are outgrowth of the gonads, therefore probably have no relation to nephridia.

16. Dinophilea.

Korschelt (1882) described for *Dinophilus apatris,* and Weldon (1887) for *D. gigas,* a nephridial system of the platyhelminthan type, though both of them saw clearly only the flame cells. Subsequent observations have demonstrated that there are metamerically arranged, separated nephridia. Thus Schimkewitsch (1895) found in *D. vorticoides* four pairs of these in the male and five pairs in the female; Harmer (1889) and Shearer (1906) for *D. tæniatus,* Nelson (1907) for *D. conklini,* and E. Meyer (1887) for *D. gyrociliatus* discovered five pairs. These are ciliated tubes each with its own nephridiopore, closed internally, and (according to Shearer) beset with solenocytes. In *D. conklini* the first pair is much more complex than the others and consists of a considerable number of cells; each of those of *D. gyrociliatus* is described by Meyer as consisting of only two cells.

Schimkewitsch considered the genital ducts of the male to be a fifth pair, and the corresponding ducts of the female to be a sixth pair of nephridia, and Harmer regarded the seminal vesicles as segmental organs. This is, however, little more than a supposition, since the genital ducts are quite different in structure from the

nephridia and are in connection with the cœlom (genital chamber), and since the development of the nephridia is unknown.

The mid-gut has also been demonstrated to be excretory (Schimkewitsch, 1884).

17. Hirudinea.

Adult Meganephridia.—There is a series of separated pairs, less numerous than the somites. Nephrostomes may be lacking as in the case of five out of the seventeen pairs of *Hirudo* (McKim, 1895) the three most anterior pairs of *Nephelis* (Graf, 1893), and all of *Branchellion* (Bourne, 1884). Leuckart (1894) discovered the anatomical connection of the nephridia with the nephrostomes, and this has been corroborated by Voinov (1896), McKim, Graf and Schultze (1883), in opposition to the results of Bolsius (1892) that the "organes ciliés" have no connection with the loop. But even when they are connected there need not be an open communication between the two (Graf, 1899). When present the funnel lies in the segment prèceding that of the loop. The cavity of the nephridia is much branched and intracellular. An excretory bladder may be present as a part of the excretory duct, but this is lacking in *Clepsine*.

The nephridia arise from segmentally arranged mesoblastic nephroblasts, that lie deep below the embryonic epidermis. Each of these divides into two cells, the anterior of which gives rise to the funnel and the posterior to a cord of cells that forms the secretory portion of the loop; the cavity into which the nephrostomes open is a true cœlom; the excretory ducts and vesicles are ectoblastic ingrowths (Bürger, 1891, 1894, 1902, Bergh, 1891, McKim, 1895). Bürger is very positive with regard to the mesoblastic origin of the nephridia, in opposition to the earlier view of Whitman (1887).

Adult Plectonephridia.—Bourne (1884) first found net-like nephridia in *Branchellion, Pontobdella* and *Piscicola;* in *Pontobdella* they consist of a network of canals extending from the ninth to the nineteenth segment, with ten pairs of nephridiopores, while in *Branchellion* they have only one pair of such openings. They have been redescribed by Johansson (1898), and I am acquainted with

his account only from the citation given by Lang (1903, p. 103). "In *Pontobdella* the nephridia consist of very richly branched and reticularly anastomosing tubes, among which one cannot distinguish main trunks. The two nephridia of the same segment are many times joined together, and the nephridia of the several segments equally so. In *Cystobranchus* each nephridium has attained a complete independence and connects neither with the other nephridia of the same segment, nor with those of neighboring segments. It consists then also only of a single, coarse, unbranched tube. The remaining genera correspond in this relation more or less with *Pontobdella;* one can, however, always distinguish particular trunks. In *Piscicola* one part of the nephridium, that is much more strongly developed than the remaining part, corresponds exactly in position with the nephridium of *Cystobranchus*. *Pontobdella* departs, finally, from all the other genera in this, that the nephridia have inner openings." Nothing is yet known of the development of these reticular organs.

Genital Ducts.—These were considered by Nusbaum (1885) to be modified nephridia. Bürger first (1894) opposed this comparison, but later (1902) he maintained that the female genital apparatus and the terminal portions at least of the vasa deferentia are possibly homologous with nephridia in developing from gonoblasts that are homodynamous with nephroblasts.

Larval Nephridia.—In the Hirudinea three of the blastomeres of the 4-cell stage give rise to a larval body that later perishes, while the fourth blastomere alone produces the adult body (Brandes, 1901). This larval body produces no nephridia. The "Urnieren" arise from the germ band that develops within this larval body, and they last only as long as the latter does. Bergh (1884, 1901) has shown that there are three pairs of these in *Aulastoma* and *Hirudo* and two pairs in *Nephelis,* all developing from the germ band; and he and Sukatchoff (1900) demonstrated that the inner ends are closed and the cavity intracellular. These larval nephridia arise from cell rows of the germ band that are generally considered mesoblastic, though this point is hardly finally settled.

Excretophores.—Excretory cells within the connective tissue

(Graf, 1899), that develop from the splanchnic layer of the mesoblast (Bürger, 1902).

Chloragogue (Botryoïdal Tissue).—Excretory cells placed upon the blood vessels (Graf, 1893).

18. Oligochæta.

Adult Nephridia.—There are two main kinds of these which it will be convenient to consider separately: *meganephridia,* larger and in separated pairs; and *plectonephridia,* networks of smaller nephridia.

Meganephridia.—Of these there is usually one pair to each trunk segment, though exceptions are very numerous; each has a preseptal open funnel and a postseptal loop with intracellular cavity; their nephridiopores are usually separated and placed latero-ventral. The smallest number known is two pairs (*Bdellodrilus,* Moore, 1897). In *Brachydrilus* there are two pairs to each somite (Benham, 1888). The anterior five pairs open into the pharynx in *Dichogaster* (Beddard, 1888*b*), and probably also in *Eminea* (according to Benham, 1890*b*, who terms this a "peptonephridium"). In *Limnodrilus* the two anterior pairs perforate septa while the others do not (Rybka, 1899). *Libyodrilus* is characterized by the nephridia opening into a tubular system situated in the musculature, consisting of four main longitudinal vessels extending from segment to segment and of segmental ring vessels, there being numerous excretory ducts from the latter; this integumental network is secondary and develops after hatching (Beddard, 1891). Numerous other deviations from the general type are known that it is not necessary to mention here, beyond the fact that nephrostomes are lacking in the Chætogastrids (Vejdovský, 1885).

Plectonephridia.—A plectonephridium is a complex that in each segment is composed of numerous micronephridia, without nephrostomes, that are joined by a network of canals. In *Acanthodrilus* there is one such micronephridium to each of the eight setæ of each posterior segment, and in each anterior segment there are about one hundred nephridiopores; somewhat similar relations obtain in *Typhæus* (Beddard, 1888*a*). In *Megascolides* there are a great number of bundles of micronephridia which clothe the body wall

except medially, these opening into a network of intracellular ducts placed outside of the peritoneum, and the latter discharge at the surface by irregularly arranged canals (Spencer, 1889). In *Mahbenus* each micronephridium has its own excretory duct (Bourne, 1894). The network of fine canals may be continuous from segment to segment, as in *Perichæta,* or only the micronephridia of one and the same segment may be so connected as exemplified by *Deinodrilus, Acanthodrilus,* and *Dichogaster* (Beddard, 1888*b*).

Both of these kinds of nephridia may occur in the same animal and even in the same segment, as in *Megascolides;* and in this genus there is a pair of ventral longitudinal canals continuous from segment to segment into which both open (Spencer). In *Dichogaster* the posterior segments contain both kinds (Beddard, 1888*b*).

Development of the Meganephridia.—With great hesitation I attempt to give a brief review of this subject, that has proved the Austerlitz of many a theory. Kowalevsky (1871) was the first to demonstrate the mesoblastic origin of these organs in *Euaxes* (*Rhynchelmis*) and *Lumbricus.* Vejdovský and Bergh have furnished more observations on the subject than any other writers. Vejdovský's results (1885, 1892*a,* 1900) on *Rhynchelmis, Stylaria* and *Tubifex* are as follows: Each nephridium arises from three separated anlages: (1) A large preseptal funnel cell, giving rise to the nephrostome; (2) a cord of small cells budded off behind the former, producing the secretory loop; and (3) an ectoblastic invagination that joins with the latter and forms the distal canal and the excretory vesicle. Bergh's studies (1888, 1890, 1899) on *Lumbricus, Criodrilus* and *Rhynchelmis* differ from those of Vejdovský mainly in deriving each nephridium from a single mesoblastic anlage instead of from three parts; in his mind the organ is essentially an embryonic unit. Wilson (1889) concluded for *Allolobophora* that the funnel arises from a large mesoblast cell, and the loop from a postseptal mass of cells that is continuous with the ectoblastic nephridial cell cords, though he admits the loop may nevertheless be mesoblastic. And Lehman (1887, *Allolobophora*) derived the nephridium from a large preseptal cell.

These researches agree in finding that the nephridia arise seg-

mentally, to which the conclusions of Roule (1889) alone are opposed, and that their first beginning is the preseptal funnel cell. But there is considerable conflict of opinion as to what germ layer produces these cells and the cords that arise behind them. They arise in that cell row of the germ band formed by proliferation of the posterior nephroblasts. The germ band is covered by a thin ectoblast, and the funnel cells lie at points where the mesoblastic dissepiments meet the ectoblast; they are blastocœlic in position. Bergh is positive that funnel cells and nephridial cords are mesoblastic, derived from what he terms the "innere Muskelplatten," and Lehmann and Roule express the same opinion. Wilson hesitates to decide whether the nephridial cords are ectoblastic, though he ascribes this origin to the funnel cells. Vejdovský considers that at this early stage of the embryo, when these parts are first definable, there is no mesoblast but only the two primary germ layers and that the funnel cells may have emigrated from the ectoblast. It is to be noted in this connection that the funnel cells when they are first distinguishable have never been seen actually in the ectoblast, but always beneath it. And the nephridial development is so correspondent with that of the Hirudinea, for which Bürger shows so convincingly that the nephridia are mesoblastic, that the view of Bergh would seem to be correct. Consequently Goodrich (1895) in his summary of the literature on this subject would seem to have misunderstood the facts of the case. We may at least conclude, that in light of the evidence at hand all the inner portion of the nephridium is mesoblastic, and only its distal outer termination comes from the ectoblast.

Remarkable postembryonic changes have been described by Rosa (1903*a*) for *Lumbricus*. In a newly hatched individual two canals extend through the whole trunk and join posteriorly into an ampulla that opens dorsally into the intestine (for which reason the describer compares it with the nephridia of Rotatoria). From each of these canals tubes branch off segmentally and connect with the nephridia of the corresponding segments, while the nephridia still lack nephridiopores; later in each segment a diverticulum grows out from each canal and opens on the surface in the position wherein the adult the nephridiopore lies, while in each segment the main

canals swell into a pair of vesicles; in the adult these longitudinal canals have disappeared, probably by segmenting into segmental excretory vesicles and nephridiopores.

Development of the Plectonephridia.—In *Megascolides* each segment has one pair of nephridial anlages, each consisting of a preseptal cell and a postseptal cord; so far the development is like that of the meganephridia; then the postseptal cord originates many loops and by a rupture of their connecting bridges the micronephridia result; the longitudinal canals connecting the latter arise later and are therefore secondary (Vejdovský, 1892*b*). In *Mahbenus* Bourne (1894) described an essentially similar process: that the funnels degenerate, that the loops form secondary and the latter tertiary branches, until each segment comes to contain about fifty micronephridia. These observations indicate clearly that the plectonephric condition is a modification of the primary macronephric by a subdivision of originally single organs. This is the position taken by Vejdovský, Bourne and Beddard (1892) which is contrary to the hypothesis of Benham (1890, 1891*a*), Spencer (1889) and Beddard (1891) that the plectonephric condition is primitive and comparable with that of the Plathelminths. Micronephridia lack nephrostomes because they are division products of the loops only, and not of the funnels. Therefore Vejdovský is probably correct in his conclusion that the micronephridia are homologous with the meganephridia, because both arise from a common anlage, comparable with the embryonic pronephridium of *Rhynchelmis.*

In *Acanthodrilus* deverticula grow out from the intestine, at a region probably anterior to the proctodæum, and join with the plectonephridia of that region of the body; this connection is secondary (Beddard, 1889, 1890, 1892).

Embryonic Nephridia.—For *Rhynchelmis* three sets of embryonic excretory structures have been found by Vejdovský (1892*a*). These are (1) "Schluckzellen," cleavage cells containing canals, which had been previously considered to digest the albumen of the egg; (2) larval pronephridia, "Kopfnieren" placed between the germ band and the ectoblast; and (3) embryonic nephridia, which later change into the definitive nephridia. Bergh (1888)

found in *Criodrilus* a pair of tubes closed internally that he called Urnieren, though on account of the lateness of their origin Vejdovský considered they are rather embryonic nephridia. Wilson (1889) described for *Allolobophora* a pair of head kidneys, and Hoffmann (1899) found these opened into the head cavity. In the opinion of Vejdovský the larval nephridia develop either from the Schluckzellen, or else come from mesenchyme of ectoblastic origin. But it is yet by no means decided from what germ layer these kidneys originate.

Genital Ducts.—It was Williams (1858) who first indicated the homology of the genital ducts with nephridia, and he held the excretory function to be secondary. Claparède pointed to the typical absence of nephridia in the genital segments as evidence that the genital ducts are modified nephridia. Then Lankester (1865), reasoning from the condition in the Lumbricids, suggested that genital ducts represent the sole traces of a ventral set of nephridia that must originally have existed together with the dorsal set in all the segments; according to this view the primitive relation would be two pairs of these organs to each segment. This idea was adopted by Benham (1886*a*, *b*) who maintained that in *Lumbricus, Titanus* and *Pontodrilus* the ventral series of nephridia disappears except those that change into genital organs, and that in *Rhinodrilus, Eudrilus, Anteus, Urochæta* and *Moniligaster* just the opposite condition obtains. But Balfour (1885), as most students after him concluded that one pair of nephridia to a segment is primitive, and that "in the generative segments of the Oligochæta the excretory organs had at first both an excretory and a generative function, and that, as a secondary result of this double function, each of them has become split into two parts, a generative and an excretory." Here it is to be recalled that two pairs of nephridia to a segment is unusual, and that only in the Lumbricidæ do both genital ducts and nephridia occur in the same segment; anatomical relations therefore do not bear out Lankester's theory. With regard to the embryogeny of the genital ducts, Vejdovský (1885) found them to arise independently of the nephridia, though he considered they might be wholly or in part homodynamous with the latter; at least the funnels

of the two he considered to have this relation. Similar results were reached by Bergh (1886), Roule (1889) and Beddard (1892). Lehmann (1887) opposed the idea of homodynamy on the grounds: (1) That two pairs of nephridia to a segment is not typical; (2) that in the embryo nephridia develop in the genital segments; and (3) that the genital ducts arise later than the nephridia. Finally there may be mentioned the view of Benham (1904) according to whom the phylogenetic series is as follows: (1) The nephridia acted as genital ducts; then (2) a special cœlomostome became added to the nephridia, forming a nephromixium; finally (3) the cœlomostome formed "its own cœlomo-duct, which may either co-exist in the genital segment with the nephridium (as in most 'terricoline' Oligochætes), or the nephridium . . . disappears from the segment during or before the development of the genital duct (as in 'limicoline' Oligochætes and *Protodrilus*). We have, then, to some extent a parallel series of phenomena analogous to those described with so much care by Goodrich in the Polychæta."

There is much in these relations that is still puzzling. But at least the funnels of both organs seem to be homodynamous since they have an approximately similar mode of growth. In the Lumbricids the two organs of a genital segment might well have arisen, as Balfour intimated, as division products of a common embryonic anlage. And in those species where nephridia are wanting in the genital segments, the genital ducts, as Vejdovský argued, are to be considered as in part at least modifications of the nephridia of such segments.

Chloragogue (*Pericardial Gland*).—This is peritoneal in origin and particularly excretory (Grobben, 1888, Rice, 1902, Rosa, 1903*a*).

Peritoneum and Cœlomic Fluid.—These have been considered excretory by Grobben (1888), who holds that the cœlomic fluid is in great part an excretory product though at the same time it has the functions of blood and lymph.

Other Excretory Organs.—Here are to be reckoned the bacteroidic cells of the connective tissues, the yellow cells of the intestine, and the amœbocytes of the blood (Cuénot, 1897).

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19. Polychæta.

Adult Nephridia.—There is usually one pair to each trunk segment. In the Phyllodocidæ, Glyceridæ and Nephthyidæ their inner ends are closed and the loops are beset with solenocytes, each of which is a cell projecting into the body cavity "containing a deeply-staining rounded or oval nucleus, attached by a sort of neck to the extremity of a thin tube which opens at its opposite end into the lumen of the nephridial canal . . . Working inside the tube and attached at its distal end is a single long flagellum, which passes far down the nephridial canal" (Goodrich, 1900). In the other families the inner end is open to the cœlom, with the exception of *Polygordius* (Hempelmann, 1906) where the first pair is closed. The nephridiopores usually open separately. Each pair of nephridia stands in relation to two segments in Archiannelids, Alciopidæ, Typhloscolecidæ, certain Nereids (Eisig, 1887), Terebelloids and Cirratulidæ (Meyer, 1887), Aphroditidæ (Darboux, 1900) and Disomidæ (Allen, 1904); in the other families, therefore in the majority of species, to only a single segment. Some of the main deviations from this type are the following:

(*a*) In Capitellids each nephridium may have several nephrostomes, there may be several pairs to a segment and they may discharge into the skin and not on the surface of the latter (Eisig, 1887). In *Lanice* and *Ploimia* the fourth segment possesses two pairs (Meyer, 1887).

(*b*) In the Terebelloid *Lanice conchilega* the three anterior pairs of nephridia connect with a pair of longitudinal canals from each of which a single nephridiopore discharges on the surface; while the four following pairs of nephridia open into a longer pair of posterior canals which end blindly at about the sixteenth thoracal segment, and each of which discharges by four nephridiopores. *Ploimia* presents quite similar relations. Meyer (1887) who described these conditions holds it probable that the longitudinal canals are formed secondarily by a meeting and fusion of separate nephridial loops, incipient stages of which are to be noted in other genera. Also in *Owenia* (Gilson, 1894) do the nephridia open into longitudinal canals, that are here described as formed by an infolding of the epidermis.

(*c*) In the Terebelloids an impervious dissepiment separates the anterior from the posterior thoracal cavity; in the former there are no germ cells, and the three pairs of nephridia have small funnels; in the posterior space, which communicates with the abdominal cœlom, occur germ cells, and there the nephridia have large nephrostomes (peritoneal funnels) for the discharge of these cells. In the Cirratulids, Serpulacea and Hermellids only the first pair of nephridia are strictly excretory, and the others serve as genital ducts (Meyer, 1887).

(*d*) In Hermellids and Serpulacea the pair of thoracal nephridia unite dorsally into an unpaired duct that opens near the anterior end of the trunk (Meyer, 1887). And in *Dybowscella* the pair of the "head" has a single medio-dorsal pore (Nusbaum, 1901).

Development of the Definitive Nephridia.—The nephrostome of *Polymnia* (Meyer, 1887) arises as a fold of the peritoneum that grows backward to join the loop; the latter developes independently, simultaneously or a little later, from retroperitoneal tissue (whether mesectoblastic or mesentoblastic was not determined) that is at first solid and later acquires a cavity; the distal excretory duct is probably ectoblastic. In *Psygmobranchus* (Meyer, 1888) there first appears in the unsegmented larva a pair of large cells in the blastocœl, apposed to the ectoblast and separated from the mesoblast, these two cells become placed between the two layers of the first dissepiment and give rise to the tubes, while there evaginates to meet each of them a peritoneal funnel. Meyer holds that all the funnels of Terebelloids must have originally been parts of dissepiments, and with the degeneration of the latter have either become independent organs or else have become grafted upon nephridia. In what is the most detailed account of any polychætous nephridium, Lillie (1905) finds for *Arenicola* that the nephridia arise segmentally and independently, entirely from the somatic layer of the mesoblast; at first they are small tubes with intracellular cavities and a minute opening into the cœlom; "the anterior region of these organs . . . together with a portion of the adjoining septum, constitutes the primitive nephrostome, from which the adult nephrostome is directly derived." The terminal vesicle is also not ectoblastic, but "is formed as a differentiation of the most posterior

portion of the primitive nephridium. There is no ectodermal invagination," but the terminal portion comes from a region where mesoblast and ectoblast join, probably from a region that was originally ectoblastic.

The work of Meyer, Fraipont and Woltereck shows that Hatschek (1878) was entirely wrong in deriving the nephridia from a continuous anlage, and in stating the adult nephridia of *Polygordius* arise as branches of longitudinal ducts of larval nephridia.

Larval Nephridia.—There is one pair of these in *Polymnia* (Meyer, 1887), each with a long flagellum placed upon the outer surface of the closed inner end, on which region follows a loop composed of two cells and then an excretory canal with intercellular cavity; these persist until the first definitive nephridia function. In *Psygmobranchus* (Meyer, 1888) there is also one pair, each composed of two cells and probably without internal opening, that open on the ectoblast and do not touch the mesoblast; they belong to the first somite (that just behind the metastomium). Meyer (1887) has figured the larval nephridia of *Nereis* as internally closed canals; Hatschek (1885) finds this structural relation in *Eupomatus*, and holds the nephridia to be mesoblastic. In *Hydroides* the head kidney opens into the proctodæum (Wilson, 1890). Drasche (1884, *Pomatoceros*) held the head kidneys to have funnels, and to be mesoblastic.

The larva about which there has been the most discussion is that of *Polygordius*. For *P. neapolitanus* Hatschek (1878) described the branched head kidney as having open nephrostomes and being joined by longitudinal canals with the trunk nephridia, a condition that has led to manifold comparisons with platodan relations. But Fraipont (1888) and Meyer (1901) found that such longitudinal canals do not exist, and that the inner ends of these tubes do not possess funnels but are beset with slender cells (solenocytes) that project into the blastocoel. Meyer described also a second pair of larval nephridia behind these, which differ from trunk nephridia only in the lack of funnels. Then Woltereck (1905) in disagreement with these writers states that the two-branched first pair of larval nephridia belong to the second somite, are mesenchymatous and degenerate entirely; while the second larval nephridium belongs

to the third somite and consists of two parts: (1) A mesenchymatous portion, composed of two "Köpfchenzellen" beset with ciliated tubes, that later degenerates, and (2) a segmental portion, at least in part ectoblastic in origin, that joins with the mesenchymatous part. Woltereck finds this second pair to become the first pair of definitive nephridia that differs from the others in the absence of funnels.

In *Polygordius lacteus* Woltereck (1902) found also two pairs of larval nephridia: (1) Hauptnephridia, close to the epidermis of the ventral hyposphere, beset proximally only with tube-cells; and (2) Seitennephridia, lined with such cells along most of their lengths. In the adult of this species also one of these pairs must persist, since the foremost definitive nephridia lack nephrostomes (Hempelmann, 1906).

The present evidence is that the head kidneys are closed internally, and Meyer accounts for this by the lack of a dissepiment in front of them from which a nephrostome could form. But while Meyer and Woltereck incline to an ectoblastic and mesenchymatous origin, Lillie concludes a mesoblastic. There is no evidence that the adult nephridia are division products of larval ones, but when there is a second pair of larval nephridia it may persist in the adult.

Provisory Nephridia.—Following on the larval nephridia and before the adult one are formed there are in the Capitellids (and so far as is known only here among the Polychæta) provisory nephridia, each of which participates in two segments (Eisig, 1887).

Relation of Genital Ducts and Nephridia.—This question has been so ably reviewed by Goodrich (1895, 1900), and his investigations have contributed so much to its solution, that I need to discuss it only briefly. Williams (1858) held that these organs are homologous, and derived from a common "viscus." Then Cosmovici (1880) concluded that the segmental organs of Annelids are of two kinds: excretory organs (organs of *Bojanus*), and genital ducts, and that the two may be separated or may be united. It is the particular service of Eisig (1887) and Meyer (1887 and later papers) to have demonstrated by their anatomical and embryological studies that the peritoneal funnels, the original genital ducts, are evaginations caudad of dissepiments, and that they may or may not

join secondarily with the nephridium proper that develops independently from retroperitoneal tissue.[3] But it is Goodrich who has made the most comprehensive comparative investigation of these relations (1895, 1897, 1898, 1900). He calls the peritoneal funnel (Genitalschlauch) a cœlomoduct, and its opening a cœlomostome; when the latter preserves its original strictly genital function it is a gonostome. According to his terminology, further, a nephridium is an excretory organ with its own inner opening, and the latter is a nephridiostome. The cœlomoducts may open on the surface of the body entirely separate from the nephridia, the primitive condition, and in this case the nephridia are purely excretory and possess small nephridiostomes; or the cœlomostomes may become secondarily grafted upon the nephridia, forming compound nephromixia which are genito-urinary and possess large funnels (cœlomostomes). These relations in the Polychætes he tabulates as follows (1900):

Nephridium closed internally.	Genital funnel distinct, but opening into nephridial canal may be acquired at maturity.	Phyllodocidæ. Glyceridæ. Nephthyidæ.
Nephridium open internally.	Genital funnel with independent external opening.	Capitellidæ. ? Nereidæ (Lycoridea).
	Genital funnel becomes connected with the nephrostome, and loses its primitive opening to the exterior.	Hesionidæ (all?). Syllidæ. Aphroditidæ. Eunicidæ. Spionidæ. Terebellidæ. Sabellidæ. Etc., etc.

Goodrich adduces the various evidence for this conclusion and adds: "Moreover, it must be remembered that the two organs are mutually exclusive; never do we find a separate genital funnel in those forms which possess wide-mouthed excretory organs; and conversely, with the one possible exception of Polygordius, never do we find Polychætes having nephridia with only small true nephro-

[3] Meyer (1890) has shown that Kleinenberg (1886) was mistaken in deriving the genital ducts from the ectoblast.

stomes without genital funnels."[4] Allen (1904) has demonstrated that in *Pœcilochætus* both kinds of organs occur, nephridia with small nephridiostomes in the anterior somites, and nephromixia with large funnels in the posterior.

Thus the evidence is convincing that cœlomoduct and nephridium are two distinct organs, with originally separate origins and functions, but that the two frequently unite to produce a compound nephromixium.

Mid-gut.—This is excretory in the Polynoidæ (Schimkewitsch, 1884), and so are the intestinal cæca in the Aphroditidæ (Darboux, 1900).

Chloragogue.—Schæppi (1894) found the chloragogue of only the peritoneum, nephridia and intrasinous connective tissue is excretory (contains guanin). In *Arenicola* some of the vessels have cæca whose walls possess chloragogue cells (Willem, 1899). For the chloragogue of peritoneal origin (peritoneal glands) Meyer (1901) uses the term "phagocytic organs."

Eisig (1887) has made the most thorough study of excretion in the Polychætes; he determined that carmine is taken up by the mid-gut, then by the peritoneum, and that the hæmolymph is the vehicle of its transport to the nephridia, blood vessels being absent in the Capitellids; it ultimately reaches also the setal glands and the skin; the skin is not excretory though it becomes the seat of excretory substances, and it is by the accumulation of such material that the skin in necessitated to undergo moults.

20. Echiurida.

Segmental Organs.—These serve mainly if not wholly as genital ducts and in *Bonellia* the male lives within those of the female. *Bonellia* has but a single one, while in *Echiurus* and *Thalassema* there are from one to four pairs. Structurally (Greef, 1879, Spengel, 1880) these are long tubes each with a nephrostome close to a nephridiopore. Nothing seems to be known of their development.

[4] Hempelmann (1906) has since shown that in *Polygordius* the nephridiostomes are too small for the discharge of the germ cells, and that the latter escape by rupture of the posterior end of the body.

Anal Tubes.—There is one pair of these opening into the most posterior portion of the intestine. On their surfaces there are numerous "Wimpertrichter," and Greef supposed these not to open directly into the cœlom, but Spengel demonstrated that they do make such a direct connection and that their ciliated lining is continuous with the peritoneum. Their function is not ascertained. From their position Spengel concluded them to be ectoblastic, but not to be homodynamous with the segmental organs. But Hatschek (1880) describes them as arising not from the rectum but from the somatic mesoblast of the telson; and according to this account they form first the Wimpertrichter, then later the external pores that lie lateral from the anus.

Larval Nephridia.—These are known only from Hatschek's account (1880) of *Echiurus;* the first origin of these "Kopfnieren" was not determined; each becomes a much branched organ with intracellular cavity, from the surface of which delicate blind capillaries grow out. Torrey (1903) was unable to find larval nephridia in *Thalassema,* and determined that in this form excretion is accomplished by certain mesenchyme cells.

21. Myzostomida.

The single pair of nephridia were first recognized as such by Beard (1894), and their structure particularly described by Wheeler (1896) and Stummer-Traunfels (1903). Their relations differ somewhat in different species: they may be separated from each other, or their open and large nephrostomes may be united, their nephridiopores may be separated or united; in one species nephrostomes appear to be absent. In some species they are purely excretory, in others also spermiducal. From their development Wheeler concluded that they originally opened on the surface of the body and not into the cloaca (their usual termination in the adult), because in one species the unpaired excretory duct opens "on the surface of the body through a papilla lying just ventral to the cloacal orifice."[5]

[5] The segmental sacs (suckers) supposed by Nansen (1885) to be nephric, have been shown by Wheeler to be probably sensory.

22. Enteropneusta.

Nephridia.—There is a left canal (or a right and left) connecting the cœlom of the proboscis with the exterior, a pair of similar canals in the collar region, and in *Spengelia* (Willey, 1899) rudimentary pores along the whole trunk. Spengel (1893) considered them to take in water from without and to subserve locomotion; Willey regarded them as having lost their former excretory function, while Bateson (1884) showed by carmine injection that the collar pores are excretory.

An ectoblastic origin of these structures was the result of the study of Spengel and Morgan (1894). But Dawydoff (1907), examining those of the proboscis in the process of regeneration, found that they develop from a peritoneal evagination that connects with an ectoblastic ingrowth, and from this concluded that they are true nephridia—a view previously reached by Schimkewitsch (1888).

The genital ducts seem to bear no relation to nephridia, and the larva (tornaria) lacks special excretory organs.

Glomerulus.—A vascular structure connected with the pericardium, considered the only excretory organ in the adult (Willey, 1899); I have not seen the original description and consequently am unable to add further details.

23. Mollusca.

Adult Nephridia.—I have not attempted to labor through the compendious literature on the anatomy of these organs, but shall simply give a brief summary drawn mainly from the excellent treatment by Hescheler (1900). These are essentially similar and homologous throughout the group, and consist typically of a pair of sacs which communicate internally by open nephrostomes (renopericardial apertures) with the cœlom (pericardial cavity), and externally by nephridiopores with the mantle cavity. They are paired in all the groups except the Gasteropods, and among the latter in most of the diotocardial prosobranchs; among living forms there is more than one pair only in *Nautilus*. They may be simple tubes, or may be twisted or excessively ramose. Functionally they may

be exclusively excretory, the usual condition, or mainly genital (*Solenogastra*), or genito-urinary.

Development of the Adult Nephridia.—According to one view the glandular portion of the nephridium arises as a peritoneal funnel, an evagination of the pericardium, this joining later with an ectoblastic ingrowth, the duct or ureter; in support of this view is the work of Rabl (1879, *Planorbis*), Erlanger (1891*a*, *Paludina*), Bütschli (1877, *Paludina*), Salensky (1885, *Vermetus*), Schimkewitsch (1888, *Limax*), Drummond (1902, *Paludina*), Ahting (1901, Pelecypods), Pelseneer (1901, *Helix*), and Stauffacher (1898, *Cyclas*). That these organs are wholly mesoblastic is the opinion of Salensky (1872, *Calyptræa*), Erlanger (1892*b*, *Bythinia*), Georgevitch (1900, *Aplysia*), and Faussek (1900, *Loligo*). The third view is that they are altogether ectoblastic: Fol (1875, Pteropods), Bobretzky (1877, *Nassa*), Joyeux-Laffuie (1882, *Onchidium*), Sarasin (1882, *Bythinia*), and Meisenheimer (1898, *Limax*, 1901*a*, *Dreissensia*, 1901*b*, *Cyclas*).

The first of these views has the greatest support, pointing to the pericardial origin of the funnel and glandular portion, and to ectoblastic origin of some portion of the ureter only. For the third view, wholly ectoblastic origin, it will be noted that the only recent work is that of Meisenheimer. Now almost all the writers conclude a common origin of the glandular portion of the nephridium and the pericardium and Meisenheimer does so likewise, but in opposition to almost all preceding study he regards the pericardium and heart as ectoblastic abstrictions. Meisenheimer must surely be incorrect in interpreting the peritoneum and with it the nephridium as ectoblastic, *i. e.*, he must have defined the germ layers quite differently from other embryologists, since the pericardial cavity is justly considered cœlomic yet in no other animal group is the cœlom regarded as lined by ectoblast.

These definitive nephridia seem to arise independently of the larval ones, save that Rho (1888) and Mazzarelli (1892, 1898) state that the mesoblastic anal kidneys of opisthobranch larvæ become transformed into the adult ones.

Genital Ducts.—"Relations between the nephridial and genital system, similar to those in the Worms, exist in the Solenogastrids

where the nephridia function as discharge ducts for the genital products. . . . And again in some Lamellibranchs, Diotocardians and the Scaphopods there exist relations between sex glands and nephridia in that the sex glands open into the nephridia, so that a shorter or longer portion of the latter functions not only as kidney or ureter but also as discharge duct for the genital products ' (Hescheler, 1900). In those prosobranchs with only one adult nephridium, Drummond (1902) has shown for *Paludina*, and after a full discussion of the literature, that the right nephridium of the embryo persists as the left one of the adult, in agreement with Erlanger, but contrary to his results she finds the left nephridium of the embryo does not disappear but becomes the genital duct.

Larval Nephridia.—These are known only in Gasteropods and Pelecypods (Lamellibranchs), and it will be most convenient to treat separately the groups in which they occur.

(*a*) *Prosobranch Gasteropods.*—Two kinds of these have been described. (1) External nephridia (Aussennieren, excretory cells). These are ectoblastic, unicellular or multicellular organs, usually projecting from the surface of the body just behind the velum; there is one pair of them, and their cavity communicates with the blastocœl; sometimes they have an opening to the exterior. They have been described most carefully for *Crepidula* (Conklin, 1897) and *Fasciolaria* (Glaser, 1905), also for *Nassa, Natica, Fusus* (Bobretzky, 1877), *Paludina* and *Bythinia* (Sarasin, 1882, who calls them "ansæ"), *Fasciolaria* and *Fulgur* (McMurrich, 1886), *Fissurella* (Boutan, 1885), and *Capulus* (Erlanger, 1892*a*). Glaser has demonstrated that they are first digestive, later serve as reservoirs for waste products, and subsequently fall off from the surface of the larva; Sarasin and McMurrich supposed they were originally parts of the preoral velum, and that with excretory specialization they separated off from it; but Conklin and Glaser show that they arise independently of and before the velum. As "secondary outer kidneys" Glaser has described certain excretory cells placed in the velum and the head vesicle.

(2) The second kind of larval excretory organs of the prosobranchs are mesoblastic. These arise from a mesoblastic anlage that is at first solid, while more or less of the duct is ectoblastic;

they are ciliated with exterior apertures. These have been found in *Bythinia* and *Paludina* (Bütschli, 1877, Erlanger, 1891*a*, 1892*b*).

(*b*) *Opisthobranch Gasteropods.*—Here there are distinguished nephrocysts and anal kidneys. The nephrocysts were discovered and named by Trinchese (1881) for *Ercolania, Amphorina, Bergia* and *Doto;* and were described also by Mazzarelli (1892) for *Aplysia* and by Casteel (1904) for *Fiona.* These are rounded bodies lying anterior to the anus in the blastocœl, without external ducts; nothing positive is known of their origin, and Trinchese supposes them mesoblastic simply from their position. They may occur in the same embryo together with the following organs. The anal kidneys were first interpreted as excretory by Langerhans (1873, *Doris* and *Acera*). They are a pair of single cells, or groups of cells, that originate near the anus but may migrate further forward. Trinchese (1881) and Guiart (1901) derived them from the mesoblast, and so also did Mazzarelli (*Aplysia,* 1892, 1898) who ascribed the occasional unpaired condition to the fusion of a pair. But Lacaze-Duthiers and Pruvot (1887) described them as ectoblastic, and this conclusion was reached also in the careful studies of Heymons (1893, *Umbrella*) and Casteel (1904, *Fiona*). Casteel's work is the most thorough on any opisthobranch, and he states: "There is no point regarding the cytogeny of *Fiona* of which I am more certain than that the group of cells constituting the anal kidney is of ectodermal origin."

(*c*) *Pulmonate Gasteropods.*—Here again there are two kinds of larval kidneys. The external kidneys (äussere Nieren) occur one on either side of the body, each a projecting group of vacuolated cells forming part of the ectoblastic velum. These were discovered by Bütschli (1877), and have been described by Fol (1880) and Rabl (1879) for *Planorbis.* Much more attention has been given to the head kidneys (Urnieren). The most detailed description of these in their perfected condition is that of Meisenheimer (1898, 1899): in the Basommatophora (*Ancylus, Physa, Planorbis, Limnæa*) these are much alike, each consisting of but four cells with intracellular cavity, the innermost of which closes the canal against the blastocœl and bears a ciliary flame. In the Stylommatophora (*Limax, Succinea, Helix, Arion*) the cells are much

more numerous and the inner end is composed of a number of large amœboid cells all of which have long cilia; for a while the inner end may be open (as described by Rabl, 1879, and Erlanger, 1894) since the cells there may become loosened from their epithelial connection, but later this end becomes completely closed even though at places by a very thin membrane. These are the most complicated larval nephridia found in Gasteropods; they subsequently degenerate completely. As to the development of these head kidneys: Rabl (1879) and Holmes (1900) considered them mesoblastic; Erlanger (1893) interpreted them as mainly mesoblastic with a portion of the duct ectoblastic, and Pelseneer (1901) stated that the large distal portion is ectoblastic. But Fol (1880), Wolfson (1880) and Meisenheimer (1898) concluded that they are entirely ectoblastic; the last named investigator speaks of them as arising as paired tubular invaginations at the level of the proctodæum.

(*d*) *Pelecypods* (*Lamellibranchs*).—In *Teredo* there is a pair of ciliated Urnieren in the young larva (Hatschek, 1880). Only the left one is developed in *Cyclas,* and opens externally in the region of the head vesicle; it consists of three highly complex cells with intracellular cavity, the innermost branched cell closing it from the blastocœl (Stauffacher, 1898). In *Dreissensia* each of the larval kidneys consists of three cells, the innermost provided with a ciliary flame and closing the canal, the next forming the tube, and the third constituting a duct connecting with the surface (Meisenheimer, 1901*a*). With regard to the embryogeny, Hatschek described these organs as appearing first at the anterior ends of the mesoblastic bands, at first with no connection with the ectoblast, and concluded that the nephridium of each side "is probably derived from only one or a few mesoderm cells"; Stauffacher held that in *Cyclas* only the innermost cells is mesoblastic and the others ectoblastic; while Meisenheimer (*Dreissensia,* 1901*a*, *Cyclas,* 1901*b*) described them as arising conjointly with the heart and pericardium from the ectoblast.

Homologies of the Larval Nephridia.—Salensky (1872) and Bobretzky (1877) homologized the outer kidneys of prosobranchs with the Urnieren of Pulmonates. Bütschli (1877) suggested that the Urnieren of *Paludina* are possibly homologous with those of

the pulmonates, but that there is no homology between the outer kidneys of these groups. Rabl (1879) concluded that the outer kidneys of *Planorbis* are probably comparable with the outer kidneys of freshwater prosobranchs, but not with the Urnieren. Fol (1880) maintained that the outer kidneys of Pulmonates are homologous with the Urnieren of prosobranchs. Erlanger (1893) regarded all the larval nephridia as homologous with each other and probably also with the head kidneys of Annelids, and distinguished the following kinds: (1) Outer ectoblastic kidneys (marine prosobranchs); (2) inner mesoblastic, and these either (*a*) purely mesoblactic (opisthobranchs), or (*b*) mesoblastic with the canal at least in part ectoblastic (pulmonates, pelecypods, freshwater prosobranchs). Mazzarelli (1904) considered the Urnieren of pelecypods, pulmonates and freshwater prosobranchs to be homologous, but the external nephridia of marine prosobranchs to be different structures; and the nephrocysts of opisthobranchs to be organs that have secondarily lost their ducts and that correspond with the excretory cells of the Urnieren of other Mollusks. Finally Glaser (1905) has given a good review of the question, and maintains there are at least three distinct and dyshomologous larval excretory organs (1) Urnieren, mesectoblastic structures of prosobranchs and pulmonates; (2) Aussennieren, modified ectoblastic cells of prosobranchs and pulmonates; and (3) excretion cells, those of *Umbrella* placed near the anus; the Urnieren are further of two kinds because some of them appear to be wholly ectoblastic.

There is so much confusion of opinion with regard to the development of even the same kind of excretory organ in the same species, that I fully agree with Casteel (1904) "that much more work must be done upon these organs of molluscan larvæ before we are ready to come to definite conclusions regarding their mutual relations and homologies, if such exist." There are certainly two distinct kinds that may occur at the same stage in the same species, and that on account of their differences in position, structure and origin are not homodynamous, and these are: (1) Projecting vesicles, wholly ectoblastic, forming part of or placed near to the velum; and (2) vesicular or tubular organs placed below the ectoblast and behind the preceding, which in most cases appear to be

in part mesoblastic. All those of the first kind may well be homologous, but those of the second kind are more probably heterogeneous structures.

Other Excretory Organs.—According to Cuénot (1899) the following structures are excretory: in the Amphineura and Scaphopoda connective tissue cells; in prosobranch and opisthobranch Gasteropoda similar cells as well as cells of the liver; in the Pelecypoda pericardial glands; and in the Cephalopoda phagocytes and the gill-hearts.

24. Tardigrada (Arctiscoidea.)

A pair of glands opening into the rectum were supposed by Plate (1888) to be excretory, and he compared them with the Malpighian vessels of the Acarina. But neither he nor Basse (1905), who has furnished a fuller description, were able to find excretory products in these organs. Nothing is known of their development.

25. Pycnogonida (Pantopoda).

Dohrn (1881) has described problematical "Excretionsorgane" within the cavity (blastocœl) of the fourth or fifth joint of the second extremity, or the third or fourth joint of the third; each has an external opening placed upon a small tubercle; in genera where the named extremities are absent, these organs are found in the wall of the body at points opposite the missing extremities. These organs lie in extremities that lack reproductive organs, and for that reason Dohrn suggested they may have some homodynamic relation to the latter.

Kowalevsky (1892) found by injections of acid fuchsine that the stain is taken up by small hypodermal glands placed in *Phoxichilus* on the borders of the three anterior segments and on the bases of extremities fourth to seventh, and in *Pallene* and *Ammothea* in the lateral processes of trunk segments and in the first joints of the extremities.

26. Crustacea.

Shell Glands (*Maxillary Glands*).—These have been described for the Phyllopoda (Leydig, 1860, Weismann, 1874, Claus, 1875, Dohrn, 1870, Nowikoff, 1905), Copepoda (Claus, 1877, Nettovich,

1900), Isopoda (Vejdovský, 1901; and Nemec, 1896, who states that in *Ligidium* they are modified into salivary glands), Cirripedia, (Bruntz, 1903, Berndt, 1903; in *Balanus* they communicate with the cœlom only in the cypris-stage according to Gruvel, 1894), Stomatopoda (Bruntz, 1903), and freshwater Ostracoda (Claus, 1895, Daday, 1895). These open at or near the base of the second maxillæ, each has a closed enlarged end sac lined by an excretory epithelium, and they are placed in the shell duplicature except in *Leptodora* where the greater portion of the organ lies in the thorax. According to Richard (1892) their ducts are longest in freshwater and shortest in brackish water species. In freshwater Cladocera (*Simocephalus*) I have found that the end sac takes up injected carmine at the end of a few hours.

Antennal Glands.—These have been described for the larvæ (but not adults) of Copepoda and Phyllopoda (Grobben, 1881), for Amphipods (Grobben, 1881, Bonnier, 1891, Bruntz, 1903, Vejdovský, 1901, Della Valle, 1893), Schizopoda (Grobben, 1881, Bruntz, 1903), Ostracoda (Claus, 1890, 1895), Cirripedia where they are modified into cement glands but may still continue excretory (Koehler, 1890), Isopoda (in *Asellus* where they are degenerate, Nemec, 1896), and Decapoda (Marchal, 1892, Waite, 1889). The antennal glands are essentially similar to the maxillary. Both have closed end sacs, are without cilia, and both (Vejdovský, 1901) possess at the junction of the gland and duct a narrow "Trichter" composed of a few large cells with a peripheral muscular sphincter.

Development of the Preceding Organs.—According to the earlier observers (Reichenbach, 1886, Ischikawa, 1885) the shell and antennal glands are ectoblastic, but other studies (Kingsley, 1889, Waite, 1899, Grobben, 1879, Lebedinsky, 1891) show that each arises as a reduced cœlomic sac (or portion of one) connecting with an ectoblastic duct. The end sac of the adult thus corresponds to the cœlomic sac of the embryo.

Maxillipedal Glands.—In *Diaptomus* there is a pair of these opening at the basis of the first maxillipeds; their structure is like that of the preceding glands (Richard, 1892). It is probable that some of the glands described as maxillary are really maxillipedal.

Coxal Glands.—In *Gammarus* (Della Valle, 1893) there are

small groups of gland cells, that take up carmine, placed at the bases of the maxillipeds, thoracic and abdominal extremities. Similar appear to be the " Segmentalorgane " of the Ostracoda (G. W. Müller, 1894), which in *Paradoxostoma* lie above each leg pair, and in *Bairdia* above the first pair; and the glands opening on the maxillipeds of Cyprids (Claus, 1890).

Genital Ducts.—The first origin of these seems to have been little investigated, but Pedaschenko (1899) finds them to arise from a proximal mesoblastic and a distal ectoblastic portion.

Homologies of the Preceding Organs.—The maxillary, antennal and maxillipedal glands are probably homodynamous, and seem to differ only in antero-posterior position. Sometimes they occur at the same time in the same individual, or (as in Phyllopods and Copepods) the antennal gland is the larval and the shell gland the adult excretory organ. Sometimes both antennal and shell glands are absent in the adult, as in some Copepoda (Nemec, 1896). Waite (1899) has discussed these homologies at some length, and resumes: " The nephridium of Annelids is *probably* represented in Crustacea in the second (antennal) segment by the antennal gland of Malacostraca; in the fifth (second maxillary) segment by the shell gland of Entomostraca and some Malacostraca; in the sixth (first maxillipedal) segment of *some* Malacostraca by the ' Segmentalorgan ' of Lebendinski; it is *possibly* represented in the fourth (first maxillary) segment by the excretory organ described by Boutchinsky, and in the sixth to thirteenth (maxillipedal and pareiopodal) segments in part by the branchial glands, and in part (in the eleventh and thirteenth segments) by the genital ducts."

Nephrocytes.—Bruntz (1903) has found these excretory cells to be distributed as follows: they are absent in the Cladocera; there is one cephalic pair in the Isopoda, Amphipoda and Cirripedia; up to eight pairs placed in the thorax in the Schizopoda, Decapoda (in the gills), and Copepoda parasitica (diffuse); from one to eight pairs in the abdomen in the Isopoda and Stomatopoda (in the legs); and eleven pairs in the thorax and abdomen in the Amphipoda.

Other Excretory Organs.—As such have been described the ferment cells of the liver of Decapoda, Amphipoda and Isopoda, and

the mid-gut cæca of Amphipoda (Bruntz, 1903); the mantle in the Cirripedia (Gruvel, 1894); and connective tissue cells of Copepoda when the antennal and maxillary glands are lacking (Nemec, 1896).

27. Onychophora (Protracheata).

Nephridia.—According to the observations of Balfour (1883) and subsequent investigators, one pair of nephridia occurs in each trunk somite, *i. e.*, one pair to each pair of legs, except in the penultimate or antepenultimate segment. Each opens ventrally at the basis of a leg, and consists of an outermost excretory bladder, a loop and a nephrostome that opens into the cœlom; but the portion of the cœlom that has such a connection is, as in the case of the antennal and maxillary glands of the Crustacea, completely abstricted from the remainder of the cœlom and with excretory function, therefore each such cœlomic sac may rightly be considered a closed inner end sac of the nephridium. This is in agreement with the facts of the embryogeny, as detailed by Sedgwick (1885–8) and Evans (1901), according to whom each right and left cœlomic sac pinches into a dorsal and a ventral portion, and the latter portion sends an outgrowth reaching to and opening at the leg.

The salivary glands and genital ducts develop like the nephridia and represent them in segments where they are lacking, are accordingly homodynamous with them (Sedgwick); and the receptaculum ovorum is homodynamous with an end sac of a nephridium (Evans).

Anal Glands.—These also have been considered homologous with nephridia by v. Kennel (1885). But Purcell (1900) has indicated that the so-called "accessory glands" of the postgenital segments may rather be dyshomologous; that while those (anal glands) of the American *Peripatus* are nephridia, those of other genera are probably ectoblastic crural glands.

Nephrocytes.—There are medio-dorsal bands of these, also masses of them near the bases of the legs (Bruntz, 1903).

28. Insecta.

Malpighian Vessels.—These are absent in Japyx (Grassi, 1888) and also in the Collembola where Folsom and Welles (1906) found that the whole ventriculus is excretory and periodically moults its epi-

thelium; they are not, as generally supposed, absent in the Aphidæ, for Witlaczil (1882) has shown that the so-called pseudovitellus represents them. In all other Insects these vessels are present, and are usually delicate, cylindrical tubes, rarely varicose or ramose, with their inner ends closed and the distal ends joining with the intestine usually at the junction of the mid-gut and proctodæum, and they may insert there singly or by one or several common ducts. In some cases there are two different kinds in the same species. Their number is often constant for a group as may be seen from the following summaries taken from the observations of Dufour (1833, 1841, 1851): in the Diptera there are usually four, rarely five (*Culex*), and never more than four in the Hemiptera; there are generally less than eight in the Coleoptera; six in Phryganids, Termes, Megaloptera (*Corydalis, Sialis*), *Panorpa,* eight in *Hemerobia* and *Myrmeleo;* they are much more numerous in the Orthoptera, Hymenoptera, Libellulidæ and Ephemeridæ.[6]

While Dufour called them "organes hepatiques ou biliaires," subsequent work has proved conclusively that they are the main excretory organs.

According to the majority of investigators they arise as evaginations of the ectoblastic proctodæum, and only in some Hymenoptera do they first appear as ectoblastic evaginations at the posterior end before the proctodæum forms. The largest number known in any embryo is ten (*Melanoplus,* Packard), which seems to be the single case not in agreement with Wheeler's conclusion (1893*a*) that no more than six occur in embryos. Wheeler concludes that six is the primitive number, while others have reasoned this to be four. Only in the Termites are they more numerous in the larvæ than in the adults.

Homologies of the Malpighian Vessels.—These have been compared specially with the sericteries and tracheæ and more generally with nephridia of the annelidan type; and it is most convenient to treat these relations at this place. Bütschli (1870) showed that the sericteries and Malpighian vessels develop like the tracheæ, re-

[6] A good review of their numerical and other relations is given by Packard (1898). In the Thysanura (except *Japyx*) their number was found by Grassi (1888) to vary from eight to sixteen.

garded the sericteries and tracheæ as homologous, but questioned whether the Malpighian vessels are related to them. Then, following Semper's (1874) suggestion that the tracheæ are metamorphosed segmental organs, Mayer (1875) went further in concluding that the tracheæ, sericteries and Malpighian vessels are homodynamous and all homologous with nephridia of Annelids. Grassi (1885) has in the main supported Mayer, in reasoning that the Malpighian vessels, sericteries, the two transitory invaginations on the head and the homodynamous tracheæ are all probably excretory in the larva; and (1888) supports the idea of the homology of Malpighian vessels with tracheæ on the ground that the former occur in segments where the latter are lacking and are most abundant when the latter are least numerous. But several strong objections have been made to these comparisons, and especially by those who have studied the embryogeny more in detail. Thus Hatschek (1877*b*) has argued against the homology of the sericteries and salivary glands with the tracheæ, that in the segments where the former occur tracheal invaginations are formed independently of them. Then Palmén (1877) concluded that the Malpighian vessels, developing from the proctodæum, were originally hypodermal glands that have come to group themselves around the inner end of the proctodæum and that their number is "in no way dependent upon the number of particular body segments"; while against the homology of the tracheæ with nephridia, he adducted the case of their coincident segmental occurrence in *Peripatus*. Wheeler also (1893*a*) judged that if the Malpighian vessels are homologous with nephridia they can be only with the ectoblastic portion of the latter; and that they are not homodynamous with tracheæ, but rather with the mass of œnocytes that represent the ectoblastic remains of nephridia. Heymons (1896) also concluded that the Malpighian vessels are not to be compared with nephridia, that they are only local evaginations of the hind-gut.

The evidence is that the Malpighian vessels are certainly not homologous with annelidan nephridia, because they are strictly ectoblastic and are not segmental. Their resemblance to the sericteries and tracheæ is only a very general one in that all of these are ectoblastic invaginations, so that at the most we must

conclude, with Palmén, that while these may all have had an essentially similar beginning no one of them has been derived from the others. The Malpighian vessels may well have been hypodermal glands that have invaginated with the proctodæum, and for this speaks their independent origin in the embryos of some Hymenoptera. In this connection it is interesting to note the conditions in the larvæ of Phryganids, as described by Henseval (1896): here there are three pairs of ventro-median glands (glands of Gilson); and Henseval regards the Malpighian vessels as homologous glands of the last segment, and the proctodæum as their unpaired portion that has secondarily joined with the mid-gut. If we omit this explanation of the proctodæum as being problematical, the comparison of Malpighian vessels with segmental glands placed anteriorly on the hypodermis might well hold.[7]

Homologues of Nephridia.—Here there are in the first instance the genital ducts, that develop as cœlomic evaginations (Wheeler, 1893, Nassonow, 1886); Wheeler has shown that all the abdominal cœlomic sacs develop such peritoneal funnels, but that only those of one particular somite reach the exterior and become functional genital ducts. He also (1893*a*) holds that the œnocytes represent ectoblastic remains of nephridia. The prothoracic gland of Dicranura has been considered homologous (Latter, 1897). Nassonow (1886) has concluded a like relation for the head glands of *Campodea,* all salivary glands, the maxillary glands of *Lepisma,* and the extensible vesicles of the Thysanura; but Oudemans (1887) and Haase (1889) combat this view and regard the extensible glands at least as not nephridial but as respiratory skin glands. Wheeler (1893*a*) considers the fat-body to represent mesoblastic remains of nephridia; some of its cells are proved to be excretory (Wheeler, Cuénot, 1895, Bruntz, 1903), and Anglas (1901) suggests that such cells compose an "accumulating kidney" that functions during the substitution of Malpighian vessels in the metamorphosis.

Nephrocytes.—According to Bruntz (1903) these cells are labial in *Machilis,* and in it as in *Lepisma* are found also on the fat-body; in larval Neuroptera on the wing muscles; in *Ephemera*

[7] Other ectoblastic glands regarded as excretory are the segmental globiform glands of *Ocypus* (Georgevitch, 1898).

on the fat-body; in the Hymenoptera, Hemiptera and Coleoptera on the pericardium; in the Lepidoptera usually dorsal in the abdomen; in the Diptera along the heart. The pericardial cells of Cuénot (1895) are perhaps to be reckoned with these.

29. Diplopoda.

Malpighian Vessels.—One pair proved to be excretory by Kowalevsky (1896) and Bruntz (1903).

Homologues of Nephridia.—Here are to be placed the genital ducts, that develop like those of *Peripatus* (Heathcote, 1888); and probably the salivary glands that are mesoblastic in origin (Heathcote), and which on account of their closed end sacs are named "rein labial" by Bruntz.

Fat-body and nephrocytes have been shown to be excretory (Bruntz).[8]

30. Chilopoda.

Malpighian Vessels.—There is one pair of these in all genera (Verhœff, 1902), and they develop as outgrowths from the proctodæum (Sograf, 1883, Heymons, 1901).

Homologues of Nephridia.—The genital ducts are mesoblastic and to be compared with nephridia (Heymons); and Herbst (1891) has described for *Lithobius* a pair of glands with thin-walled end sacs opening behind the second maxillæ, and has suggested that these may be modified nephridia. The salivary glands are ectoblastic and not to be compared with nephridia (Heymons, 1898).

31. Symphyla (Scolopendrella).

There is one pair of Malpighian tubules; the ventral sacs are simply respiratory skin glands (Haase, 1889).

32. Pauropoda.

Malpighian Vessels.—There is one pair of these in *Eurypauropus* but apparently only in the female (Kenyon, 1895). In *Pauropus* they are absent (Schmidt, 1895), and in this genus there are groups of cells in the fat-body that may be excretory (Kenyon).

[8] Haase (1889) has demonstrated that the ventral sacs are neither excretory in function nor nephridial in origin.

33. Xiphosura (Limulus).

Coxal Glands.—A very thorough account has been given by Patten and Hazen (1900). The adult gland consists of four nephric lobes at the bases of the second, third, fourth and fifth legs, respectively, and these are connected medially by a stolon of collective tubules; the duct lies dorso-lateral from the latter, is much convoluted and opens at the basis of the fifth leg. The duct arises from a plate of cells of the somatic mesoblast of the fifth somite, this plate invaginating to produce a funnel opening into a thin-walled end sac that represents the fifth cœlomic sac; the distal end of the duct is formed by an ectoblastic invagination. Outgrowths of the end sac finally unite with cell chains of adjacent nephric lobes. In each of the six thoracic somites a mass of nephric cells arises independently of the duct from the somatic mesoblast, and these masses, of which the first and sixth ultimately disappear, form the nephric lobes; offshoots from the four persisting masses produce the canals of the stolon. Thus there are in the embryo six pairs of coxal glands, but only four of them persist in the adult.

The *genital ducts* arise as deverticula of the opercular mesoblastic sacs, and are to be compared with nephridia (Patten and Hazen).

34. Arachnida.

(1) *Araneida.*

Malpighian Vessels.—These are excessively dendritic and their delicate end branches form a fine felt-work around the liver lobes; by a pair of main ducts these open into the intestine just anterior to the rectal vesicle. They have been proved to be excretory (Marchal, 1889, Bruntz, 1903). Balfour (1880) and Morin (1888) described them as arising from the ectoblastic proctodæum; but with the exception of Kishinouye (1890, 1894) who derived them from the mesoblast, the other embryologists (Loman, 1887, Schimkewitsch, 1897) find that they develop from the entoblastic mid-gut. Locy (1886) described them as coming from the prester-coral tube, but though the latter is probably entoblastic its origin was not definitely settled. Renewed investigation is needed on this question, but the entoblastic origin seems to be best authenticated.

Coxal Glands.—Evidently these are not functional but are degenerate in the adult; Bruntz (1903) has proved they are excretory. In the young of *Atypus* there is a pair of these opening on the third coxæ (Sturany, 1891), but the duct is lacking in the adult (Sturany, Bertkau, 1885). In the young of *Mygale* Loman (1888) states it is degenerate, while Pelseneer (1885) finds no ducts but on each side of the body a four-lobed gland corresponding to the four extremities of the thorax. Sturany and Hansen and Sörensen (1904) state that in the Tetrapneumones it opens behind the fifth extremity (third leg) and in the Dipneumones behind the third (first leg). Kishinouye (1890) maintained that these organs arise from the ectoblast, though he showed that the anlage opens by a funnel into the cœlom.

Genital Ducts.—Purcell (1895) has shown that these arise as evaginations of the cœlomic sacs; "the similarity of their development with that of the coxal glands in Arachnids generally indicates their nephridial origin."

Hind-gut.—This is said to serve as an excretory organ until the Malpighian vessels are developed (Bertkau).[9]

(2) *Scorpionidea.*

Malpighian Vessels.—These are branched, four in number (Dufour, 1854); though generally supposed to have the same function as those of other arachnids they are stated by Bruntz (1889) to be not urinary. They arise from the entoblastic mid-gut (Brauer, 1895).

Homologues of Nephridia.—The genital ducts develop like and are homodynamous with the coxal glands (Brauer, 1895). The latter are in one pair and open behind the fifth extremity (third leg); Bruntz has shown that they have an excretory function. These have each a narrow duct and an enlarged inner end sac. Bernard (1893) held these glands to be ectoblastic, independent of the cœlom, homologues of acicular glands. But the researches of Laurie (1890), Sturany (1891) and Brauer (1895) have demonstrated that they arise each as an outpushing of the somatic mesoblast that

[9] The spinning glands are ectoblastic, and may be equivalent to crural glands, but are neither excretory nor nephridial.

reaches to and opens upon the skin, then later loses this opening; Brauer found that a series of them arise, in segments third to sixth, inclusive, but that all but those of the fifth segment soon disappear.

(3) *Cyphophthalmidea.*

Malpighian Vessels.—There is one pair of these in *Gibocellum,* opening at the junction of the mid-gut and hind-gut; they are of great size and each is remarkable in having a net-like branching at its middle only (Stecker, 1876).

Coxal Glands.—Sturany (1891) holds what Stecker called "Speicheldrüsen" to be probably coxal glands; there is one pair of them on the sides of the stomach.

(4) *Phalangida.*

There are here no Malpighian vessels, and their absence is due, according to Loman (1888), to the functional persistence of the coxal glands. The latter are organs with an inner closed end sac (Faussek, 1892), that open in the Opiliones laniatores behind the third, and in the Opiliones palpatores and Chelonethi behind the fifth extremity. They develop as mesoblastic outgrowths of the particular extremities in which they are placed (Sturany, 1891, Faussek, 1892).

(5) *Pseudoscorpionidea* (*Chernetidæ*).

Here also there are no Malpighian vessels. The coxal glands are stated to have no exterior openings, to lie at the base of the fifth extremity, and to be of mesoblastic (nephridial) origin (Sturany, 1891). The spinning glands that have two pairs of opening on the chelicera are considered by Bertkau (1888) to be homologous with them.

(6) *Solifugæ* (*Galeodidæ*).

Malpighian Vessels.—These are one pair of branched tubes.

Coxal Glands.—There is one pair placed between the third and fourth coxæ; Bernard (1893) considered the end sacs to be prolongations of the ducts, but his account is not convincing. Loman (1888) has suggested that the poison glands are homologous with them.

(7) *Microthelyphonida* (*Palpigradi*).

There are no Malpighian vessels but the adult excretory organs are the coxal glands, and have been described by Rucker (1901) and Börner (1904). There is one pair of these extending forward from the third abdominal segment to their opening between the second and third legs; the great size of these Börner gives as the explanation for the loss of Malpighian vessels.

(8) *Pedipalpi* (*Thelyphonida*).

Malpighian Vessels.—According to Börner (1904) there is one very ramose pair of these; they develop from the entoblastic stercoral pocket near its posterior end (Laurie, 1894).

Coxal Glands.—These are strongly developed, function in postembryonic life, and their ducts open on the third pair of coxæ (Börner).

(9) *Acarina.*

My account of this group is necessarily very defective because for the most part I have seen only reviews of the literature.

Malpighian Vessels.—These seem to be absent in many species, but a pair of them has been described for *Ixodes* (Wagner, 1894), Gamasidæ (Michael, 1892, Winkler, 1888), *Halarachne* (Kraemer, 1885), and Tyroglyphidæ (Nalepa, 1884, 1885, Haller, 1880). In the nymphs of Gamasids these penetrate deep into each leg. For *Bdella* Karpelles (1893) has described an unpaired excretory organ of entoblastic origin opening into the rectum.

Caudal (*Proctodæal*) *Excretory Organs.*—These are urinary structures opening at the posterior end of the trunk without connection with the mid-gut, and are tubular or saccular, closed internally. These may be present (1) when the intestine is provided with an anus, as in *Hydrodroma* (Schaub, 1888); or (2) when the mid-gut ends blind and has no anus, as in Prostigmata (Thor, 1904), Gamasidæ (Michæl, 1892, 1895), and *Trombidium* (Croneberg, 1879, Henking, 1882). The suggestion was made by Thor that the second type probably represents a rectal bladder with Malpighian vessels that have become separated from the mid-gut. But the first type, that has an opening separate from the anus, can-

not have been so formed, but would rather seem to be ectoblastic like the Malpighian vessels in Insects.

Unicellular Glands of the Intestine.—Nalepa (1888) has described for Phytopids three large unicellular glands in connection with the rectum, and supposed they may be excretory.

Coxal Glands.—In *Limnocharis* Thon (1905) found a pair of glands in the region of the second coxæ; in *Eulais* they are most active in the nymphal stage while they degenerate in the adult (by substitution of the proctodæal organ), but in *Limnochares* they function even in late life. Supposed coxal glands have also been described by With (1904) for the Notostigmata, by Sturany (1891) for *Trombidium,* by Winkler (1888) for Gamasidæ, and by Michæl (1883) for Oribatids. The lateral abdominal glands of Gamasids, Tyroglyphids and Oribatids may be homodynamous. The development of these various glands seems to be quite unknown, so that nothing can be said of their homologies.

35. Leptocardii.[10]

The nephridia in *Amphioxus* were discovered by Weiss (1890) and particularly described by Boveri (1892). The latter found them to be segmentally arranged, in about ninety pairs in the branchial region, there being one pair to every two branchial arches. Each nephridium was described by Boveri as a canal with one opening into the ectoblastic atrium, and several into the cœlom (subchordal cavity); inserting into the orifice of each of these nephrostomes, but not into that of the nephridiopore, is a tuft of long Fadenzellen. Goodrich (1902) has reinvestigated these organs, and while he confirmed the preceding account in most particulars, he found that the Fadenzellen are solenocytes, each hollow with a long cilium and each closed from the body cavity, and that there are no open communications of nephridia with the cœlom: "These tubules are situated 'morphologically' outside the cœlom, being covered with cœlomic epithelium; the solenocytes alone push through into the cœlomic cavity." And he concluded "that in their

[10] The Leptocardii exhibit so many morphological peculiarities that they are to be removed from the group of the Vertebrata; the Craniota by themselves compose a homogeneous assemblage.

segmental arrangement, in their function, and in their histological structure, the excretory organs of *Amphioxus* and the nephridia of *Phyllodoce* are in all essentials identical." In a second communication Boveri (1904) maintained the occurrence of true nephrostomes, and held the solenocytes to be modified peritoneal cells and not to be covered by a peritoneal investment.

Unfortunately nothing is known of the development of these structures.

36. Vertebrata (Craniota).

With regard to the excretory organs of this group I shall deal reather summarily, because they have been much more studied than the excretory organs of other animals, and because most of the larger contributions on the subject deal extensively with the literature.

Nephridia.—Good reviews of the embryogeny of these structures have been presented particularly by Rückert (1892), Boveri (1892), Wheeler (1899) and Brauer (1902). There are three kidney systems which occur in the ontogeny in the order of their naming; the pronephros, mesonephros and metanephros. The first two occur in all vertebrates, the third in amniotes only. The pronephros is purely an embryonic structure except in *Bdellostoma, Lepidosteus* and some Teleosts (*e. g., Fierasfer*) in which it functions also in the adult. The mesonephros is the adult kidney of all other anamniotes, and the metanephros of the amniotes. All these organs are paired and segmented.

Pronephros.—This develops in the anterior trunk segments as serial solid thickenings of the somatic mesoblast, each of which secondarily becomes tubular and pushes towards and opens into the cœlom. Their lateral ends unite to form the collecting tubule. The arterial connection is in most cases by a paired glomus, an unsegmented vascular inpushing of the dorsal peritoneum medial from and opposite the nephrostomes. The duct, generally known as the segmental duct, also as the pronephric or Wolffian duct, arises just lateral from the tubules and grows back from them to open into the cloaca; in the Selachii and Mammals, possibly also in *Lepidosteus,* it is ectoblastic and joints secondarily with the tubules; in all other forms it arises from the somatic mesoblast in conjunction with the

tubules and like them is at first solid. Some of the more important papers on the development of these structures are the following: for the Amphibia, Fürbringer (1878), Mollier (1890), Field (1891), Semon (1891), and Brauer (1902); for the Cyclostomes, Wheeler (1899), Price (1897); for the Selachii, Balfour (1881), Van Wyhe (1889), Rückert (1888), Rabl (1896); for the Teleostei, Hoffmann (1886), Henneguy (1888), H. V. Wilson (1891), Swæn and Brachet (1901); for the Ganoidei, Parker and Balfour (1882), Beard (1889); for the Reptiles, Hoffmann (1889), Gregory (1900); for Aves, Sedgwick (1881), Balfour (1881), Renson (1883), Felix (1891); and for the Mammals, Spee (1884), Flemming (1886), Kollman (1891), Martin (1888).

Mesonephros.—These tubules develop usually in the segments behind the pronephroi, but there are certain segments that may contain both of them, and they are more numerous and more differentiated that the pronephroi. To understand their origin it is necessary to recall that the cœlom becomes divided into the dorsal myocœls (cavities of the myotomes or somites), the middle nephrocœls, both of these being segmented and paired, and the large unsegmented hypocœl that is imperfectly paired; these relations were established particularly by Van Wyhe. Very early the myocœls pinch off from the nephrocœls, whereby the latter are left as short tubes, the dorso-lateral end of each ending blindly while the ventral opens into the hypocœl. These peritoneal nephrocœls become the mesonephroi and grow laterad to join with and open into the segmental duct, for they develop no duct of their own. The arterial connection is segmental: From the aorta a vessel grows towards each tubule and ends in a capillary glomerulus against the wall of the latter above the nephrostome; the wall of the tubule forms a partial sheath (capsule of Bowman) around the glomerulus, In *Petromyzon* there is a larval as well as a definitive set of these tubules, and there may be several in each segment (Wheeler).

The principal studies on the mesonephros are these: For Selachii, Rückert (1888), Van Wyhe (1889), Rabl (1896); for Teleostei, Felix (1897); for Cyclostomata, Wheeler (1899), Price (1897), Maas (1897); for Amphibia, Semon (1891), Brauer (1902), Hall (1904); for Reptiles, Gregory (1900), Mihalkovics (1885), Wieder-

sheim (1890); for Aves, Sedgwick (1880), Felix (1891); and for Mammals, Janosik (1887), Martin (1888), H. Meyer (1890).

Metanephros (Kidney of Amniotes).—This consists of the duct or ureter, and the kidney proper, both developing behind the mesonephros. The ureter is a dorsal outgrowth from the segmental duct. There are two views concerning the origin of the glandular kidney. According to the first and older of these the kidney tubules arise as evaginations from the anterior end of the ureter (Kölliker, 1861, Waldeyer, 1870). There is much more evidence for the second view, origin independent of the ureter from mesoblastic tissue (Emery, 1883, Hoffmann, 1889, Wiedersheim, 1890). The ureter grows forward into an embryonic cell mass known as the kidney blastema, of somewhat uncertain origin, but possibly homodynamous with the anterior mesonephric anlage (Wiedersheim). According to the description of Emery (1883) the so-called collective tubules of the kidney arise as blind outgrowths of the ureter, and these join with the secretory tubules that arise independently from the kidney blastema. There is still much to be decided concerning the exact method of formation of the kidney, but certainly a considerable portion of it arises independent from the ureter from somatic mesoblast. Each tubule of the metanephros commences proximally with a Malpighian corpuscle, that is, a vascular glomerulus enclosed in a capsule of Bowman, a vascular relation like that of the mesonephroi; metanephric tubules lack nephrostomes or other connections with the cœlom.[11]

Relations of these Nephridial Systems.—That the pronephros and mesonephros are homodynamic is the view of Balfour (1881), Sedgwick (1881), Price (1897) and Brauer (1902). Field (1891) argued that the two are differentiated parts of one ancestral organ, that differ structurally because they develop at different periods. But the majority of investigators hold them to be not homodynamous, and here may be mentioned W. Müller (1875), Fürbringer (1878), Van Wyhe (1889), Rückert (1892), Semon (1891), Rabl (1896), Wheeler (1899), and Maas (1897). If we omit the conditions in the Gymnophiones in which the relations of the pronephros

[11] Adult mesonephric tubules may still maintain their nephrostomes, or may lose them; cf. Spengel, 1876.

appear strongly modified or at least quite different from those in other groups, then it is highly probable that these two organ systems are not strictly homodynamous. For the pronephroi arise as solid thickenings of the somatic mesoblast, that later become tubular and only secondarily join with the cœlom; and their vascular supply is an unsegmented glomus opposite their nephrostomes. On the other hand the mesonephroi are abstricted portions of the cœlom (nephrocœls), they are from the start peritoneal and in open communication with the cœlom; and the vascular connection of each is a Malpighian corpuscle. The pronephroi are retroperitoneal, the mesonephroi, peritoneal funnels in the main; the former develop in close connection with the segmental duct, while the latter arise much later than it and join it secondarily. In view of these differences pronephros and mesonephros are probably only incompletely homodynamous.

As to the metanephros, its ureter being an outgrowth of the segmental duct is a new structure; while the glandular kidney arises from mesoblast that may represent a late generation of mesonephric tubules. Accordingly, the metanephros can be only in part homodynamous with the mesonephros.

Homologues of Nephridia.—Here are to be placed the genital organs that I will treat very briefly. Particular genital ducts are absent in the Cyclostomes, *Læmargus* and certain Teleostei; here the genital cells fall into the cœlom and are discharged through peritoneal canals, supposed peritoneal funnels (Weber, 1886), the development of which has not been studied.

In the males of Teleosts and certain other fishes the genital ducts are simply outgrowths of the gonads, while in all other forms the segmental ducts (or portions of them) are urogenital. The vasa efferentia of the testis, the paradidymis and the hydatid of Morgagni are modified mesonephric tubules.

In the females of all forms except most Teleosts and *Lepidosteus,* where the ducts are outgrowths of the gonads, the oviduct (with uterus when present) is distinct from the urinary canal (segmental duct or ureter) and is known as the Müllerian duct. This is paired and arises in the Selachii as a longitudinal abstriction of the segmental duct, but in other forms as a structure independent of the

latter, *i. e.*, as a longitudinal peritoneal groove, showing sometimes (Reptiles) traces of segmental origin, that becomes a tube closed from the cœlom except at its anterior end (ostium). These two kinds of Müllerian ducts cannot be homologized, for the first is an abstriction from the segmental duct, while the second arises as a peritoneal infolding and may be compared with an elongated peritoneal funnel or with a series of them. The ovaries differ from testes in lacking vasa efferentia connecting them with the ducts, but other remnants of mesonephric tubules are found in amniotes in form of the epoöphoron and paroöphoron.

Other Excretory Organs.—The liver forms urea, while the sudoriparous glands, respiratory organs and skin aid in the discharge of waste substances.

B. GENERAL COMPARISONS.

I. Main Types of Excretory Organs.

We use the idea homology to denote that relation between a certain organ of one animal and a certain organ of another, which is dependent upon derivation from a common ancestral organ. In other words, homology denotes community of descent of parts. To elucidate such relations, to demonstrate change of both form and use of parts, is the first object of comparative anatomy; later all such knowledge may be so compounded as to give the general history of phylogeny. When one considers such manifold and diverse organs as those that subserve excretion, difficulties of interpretation that are almost insuperable arise to perplex and bewilder, yet at the same time compel, the attention. Any conclusions with regard to the homologies of these organs must be tentative because our knowledge of them is so very imperfect; in fact for most of the animal groups only the outlines have been made known. Therefore the following attempt to arrange the excretory organs according to their genetic relations should be regarded as only an essay.

The criteria of homology are still a matter of dispute. I have discussed this matter in another place (1906), and will simply state here that similarity of relative position to other parts seems to be the surest criterion, together with general similarity in mode of

ontogenetic formation. We shall place first relative position with regard to the outer skin, the blastocœl and cœlom, the intestine and the genital organs. These relations involve genetic connections with the particular germ layers, and a word of discussion may be in place with regard to these. The concept of the essential homology of the primary germ layers has been many times attacked since its formulation by Huxley and Kowalevsky. Yet these objections have been weakened by much of the more recent work. Ectoblast always furnishes nervous elements, entoblast originates digestive and assimilative parts, from the mesoblast come the reproductive cells; these are cardinal distinctions that seem to hold throughout the Metazoa. Therefore it is no valid objection to the idea of the homology of these layers to cite the observations of Chun on Ctenophores, that in the process of gemmation an ectoblastic outpushing gives rise to both ectoblast and entoblast. This observation can rather prove only that such an ectoblastic bud is not purely ectoblastic but mixed in its nature. And when Heymon's studies on Insects, resulting in the completely ectoblastic formation of the whole intestine, are brought up as an objection, it may be answered that the observational distinction of the germ layers in insects is very difficult, and also that these conclusions have not been corroborated by all subsequent examiners. The oft-cited case of the Trematodes, to the effect that the embryo throws off its whole ectoblast, must now be allowed to drop since Goldschmidt has demonstrated that it is not the true ectoblast but only a follicle cell layer that becomes so moulted. For these and other reasons those critics are becoming fewer who maintain that ectoblast is not always homologous with ectoblast, and entoblast with entoblast throughout the Metazoa; and the most painstaking of all embryological work, that on cell-lineage, bears out most strongly the well-founded general homologies of these primary layers. The discussion has shifted rather to the significance of the mesoblast, the existence of which was so stoutly denied by Kleinenberg. This long and wearying discussion has brought out the result, first clearly stated by Meyer, that two kinds of mesoblast are to be sharply distinguished, the primary or mesectoblast, and the secondary or mesentoblast. The

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probable correctness of this distinction is amply substantiated by the cell-lineagists, and the arguments for it have been well presented by Torrey. The mesectoblast is of ectoblastic origin, it is in part equivalent to the mesenchyme of the Hertwigs; it forms larval and to less extent adult structures, but never gives rise to germ cells. The mesentoblast form adult structures and contains the germ cells. These again are fundamental differences, so that it is no longer sufficient to state a part is mesoblastic, it is necessary to know whether it is mesectoblastic or mesentoblastic. The mesectoblast is in reality an emigrant or delaminant of the ectoblast, it is genetically related with that layer and not with the mesoblast.

Relation of position to, and origin from, these four embryonic layers gives then a primary criterion for deciding the homologies of the excretory organs. And these relations of position involve also place-relations with regard to the primary cavities of the body: The blastocœl, the space between ectoblast and mesoblast; the cœlom, the space lined by mesentoblast; and the gastrocœl, the space lined by entoblast.

Using the relations of position and origin as of primary importance, and anatomical and histological relations as of secondary, we will proceed to arrange the excretory organs in genetic groups. Many of the organs described in the preceding part of this paper could not be entered here on account of the insufficiency of our knowledge concerning them; and some others have to be marked doubtful for the same reason. It is at the best a hazardous undertaking to classify other men's results, and the danger is multiplied when descriptions are imperfect.[12]

(*a*) *Wholly Ectoblastic Excretory Organs, not Opening into the Cœlom and not Serving as Genital Ducts.*

1. Hypodermal skin glands. These are perhaps the most primitive excretory organs, and are of wide distribution. Excretory function of them has been proved for Pycnogonids, Insects, Arachnids, Vertebrates and certain others; but probably most hypodermal glands are rather secretory than excretory.

[12] Here may be mentioned a generalized embryonic excretory organ, the blastocoel, which Kofoid has shown to have the value of a discharging vesicle and to continue that function up to the gastrula stage; Meisenheimer has accepted Kofoid's conclusions.

2. Evaginated vesicles, open to the blastocœl. Here are to be reckoned the outer nephridia of prosobranch and pulmonate molluscan embryos, and probably the anal kidneys of opisthobranchs. The latter have a method of formation similar to that of the others, but they differ in position.

3. Tubular invaginations terminating blindly in flame cells, with the cavities of at least the capillaries intracellular. Their origin from the ectoblast has been proved only in the case of the Nemertini and Acanthocephala and with some doubt in the Polycladidea. Here are to be placed the definitive nephridia of the Platodes, Nemertini, Gastrotricha, Rotatoria, *Rhodope,* Acanthocephala, and the larval nephridia of *Phoronis;* probably those of the Endoprocta should be placed here (if they are not mesectoblastic), and perhaps those of the Priapulida and the head kidneys of some Molluscan larvæ. This type of excretory organ has been named by Hatschek (1888) protonephridium, though he extended this term to cover also organs of mesectoblastic and even mesentoblastic origin. This is a very natural group of excretory organs, showing great similarity in both structure and development. The only case of a larval or head kidney among them is that of *Phoronis,* yet here this kidney persists into the adult though it later joins with a cœlomostome. Kaiser (1892) is inclined to compare the organs of the Acanthocephala with those of Annelids or even with the anal kidneys of *Bonellia,* but their strictly ectoblastic origin renders this view unlikely; while those of the Acanthocephala open into the genital ducts, so also do those of certain Turbellaria, consequently this relation does not speak against their community.

4. Tubular invaginations with wholly intercellular cavity, without flame cells of cilia. These are the Malpighian vessels of Insects and Chilopods (? and of other Myriopods), the proctodæal organs of the Acarina, and possibly the rectal tubes of the Tardigrada. All of these either open into the proctodæum or upon the surface of the body near the anus; it is probable they secondarily acquired the proctodæal position when the ectoblast invaginated to produce the end-gut. These tubes are usually unbranched, but in some Insects they are dendritic. They differ from type 3 mainly in lacking cilia and in possessing a wholly intercellular cavity; but the

lack of ciliated epithelia is a histological characteristic of the groups that possess them.

(*b*) *Mesectoblastic Organs.*

Here are to placed the following structures:

5. Scattered excretory cells, such as connective tissue elements of the Mollusca, and possibly the bacterioidic cells of the Oligochæta.

6. Closed vesicles, the kidney sacs of Tunicata, and possibly the nephrocysts of nudibranch Mollusca. These seem to act as centers of accumulation of waste substances.

7. Tubes communicating with the exterior, the inner ends blind and terminating with a flame cell or solenocytes. In all probability the larval nephridia (head kidneys) of Oligochæta and Polychæta belong here (in the latter sometimes a portion of the duct is strictly ectoblastic); possibly the nephridia of the Dinophilea fall also into this category, but nothing is known as yet of their development. In their structure these are very similar to the organs of type 3, the protonephridia in the restricted sense, the only difference being that the one come directly from the ectoblast, the others from the mesectoblast.

(*c*) *Organs Wholly or Partially Mesentoblastic.*

These represent the more specialized kinds of excretory organs, correspond in part to the metanephridia of Hatschek, and may be subdivided into the following main types:

8. An ectoblastic invagination joining directly (without participation of retroperitoneal mesentoblast) with a cœlomostome (peritoneal funnel), the involved portion of the cœlom not exclusively excretory. Examples are the adult nephridia of *Phoronis,* and the head and collar pores of the Enteropneusta; homologous with these is the stone canal of the Echinodermata. The present evidence does not allow us to decide whether the segmental organs of the Sipunculida, Ectoprocta, Brachiopoda, Echiurids and Myzostomes belong with this type or with type 11.

9. An ectoblastic invagination joining directly (without participation of retroperitoneal mesentoblast) with a reduced cœlomic sac, the latter being an exclusively excretory end sac. There are

two main kinds of these: (1) The ectoblastic portion very small, and the end sac representing only a portion of the cœlom of a segment, as in the case of the salivary glands, nephridia, and genital ducts of the Protracheata. And (2) the ectoblastic portion relatively larger, the end sac being a whole cœlomic sac, as in the case of the coxal glands of Arachnids, Xiphosura, Crustacea, the salivary glands of Diplopods, and the antennal, maxillary and maxillipedal glands of Crustacea.

10. An ectoblastic tube joining with retroperitoneal mesentoblast, the latter neither joined with a cœlomostome nor serving as a genital duct; the inner end is either quite closed or else has a small opening (nephridiostome) into the cœlom; the cavity is usually intracellular. Here belong the larval nephridia of the Hirudinea, and the definitive nephridia of the Hirudinea, Oligochæta and some Polychæta (Phyllodocidæ, Glyceridæ, Nephthyidæ, Capitellidæ, and perhaps the Nereidæ). Probably the anal kidneys of Echiurids belong here, and perhaps also the nephridia of the Nematoda. In essential agreement with this type is the pronephros of the Vertebrata, which also consists of a retroperitoneal mesentoblastic tube whose inner end opens secondarily into the cœlom (not by a peritoneal funnel) and whose outer end joins with the segmental duct that is of either mesentoblastic or ectoblastic origin. Possibly the nephridia of the Leptocardii are also homologous, as Boveri has suggested, but nothing is known of their development; it will be recalled that Boveri homologized the atrial chamber of the Leptocardii with the segmental duct of the Vertebrata.[18] There is no homology between the segmental duct of Vertebrates and the longitudinal canals of the Polychætes *Lanice* and *Ploimia,* for the latter seem to be formed by a late fusion of the secretory portions of the

[18] As to the phylogeny of this segmental duct, Balfour considered it to be the foremost modified pronephric tubule, and Field has accepted this view. Haddon (1886) and Beard (1887) suggested that the pronephroi first opened separately into an open ectoblastic groove, that later closed to become the segmental duct. Rückert (1888) also concluded that originally the pronephric tubules opened independently to the exterior, and that they extended through the whole trunk; he maintained that the segmental duct arose by the meeting and fusion of their lateral ends, that is, by a backward growth of collective tubules.

nephridia. Indeed, the segmental duct of Vertebrates appears to have originated in this class.

11. An ectoblastic tube (though this portion may be very small) joining with retroperitoneal entomesoblast, and the latter connecting with a cœlomostome; these are generally either urogenital or homodynamous with genital ducts, and the cavity is usually intercellular. The inner end is widely open at least in the embryo. These correspond to type 10, with the addition of a cœlomostome. In this type fall the nephridia of the Mollusca, and those of most Polychæta. As mentioned above, the segmental organs of the Sipunculida, Ectoprocta, Brachiopoda, Echiurida and Myzostomida probably belong either here or with type 8. Essentially homologous are the mesonephroi, therefore probably also the metanephroi, of the Vertebrates, which consist to great extent of peritoneal funnels. And Boveri has argued that the gonads of the Leptocardii may be homologous with these mesonephroi.

12. Non-tubular peritoneal differentiations of excretory nature. Here are the so-called ciliated funnels of the Holothurians, that are not funnels (cœlomostomes) at all, and the widely represented peritoneal glands (phagocytic organs, chloragogue *in parte*).

13. Non-tubular retroperitoneal mesentoblastic cell masses. With these belong a variety of structures the development of most of which has been little examined, such as the excretophores of the Hirudinea and the fat-body of Insects (the latter perhaps representing, as Wheeler has suggested, the remains of nephridia).

(*d*) *Entoblastic Excretory Organs.*

14. These are relatively few in number and seldom have an exclusively excretory function. In the first place there are tubular evaginations of the mid-gut, as the Malpighian vessels of Arachnida, then the mid-gut cœca of the Polycladidea and Amphipoda and probably of the Arachnida; these are all essentially homologous. The whole mid-gut has been shown to be excretory in the Collembola, *Dinophilus* and the Ectoprocta; it seems to be specially so only when other excretory organs are wanting, and in that case there is either periodical moulting of the lining of the mid-gut

(Collembola), or when this fails there is rapid death of the individual from poisoning of the intestinal tract (Ectoprocta).

2. Homologies of the Preceding Types.

The entoblastic type (14) is *sui generis* and not related to the others. Types 12 (peritoneal glands) and 13 (retroperitoneal differentiations) are so generalized in both structure and function, that it is hardly advisable to attempt to draw homologies between them; and the same holds for types 1 (ectoblastic skin glands), 2 (ectoblastic vesicles), 5 (scattered mesectoblastic cells) and 6 (mesectoblastic vesicles). There remain then for consideration all those distinctly tubular organs, nephridia proper, into the composition of which entoblast does not enter.[14] The earliest and most uniform of these are those of type 3, ectoblastic invaginations terminating in flame cells, which are referable, as argued by Lang, to still simpler skin glands. Type 4, ectoblastic invaginations like 3 but without cilia, are essentially similar; for no one would hesitate to homologize the mid-gut of the Turbellaria and the Insects, though the former is ciliated and the latter is not; therefore one should not object to drawing homology between the water vascular system of the former and the Malpighian vessels of the latter. The lack of cilia is not a characteristic merely of these vessels, it marks all the tissues of the Insects. The only differences between types 3 and 4 is the lack of cilia in the latter, and this is a difference that is of little homological importance, a merely histological character. And essentially similar to both of these is type 7, tubes of mesectoblastic origin; they do not come immediately from the ectoblast, but from tissue of ectoblastic derivation which is but a step removed. These three types, accordingly, 3, 4 and 7 are anatomically and embryologically essentially alike, they are to be considered homologous; they stand in no relation to the cœlom, never conduct the genital prod-

[14] The term nephridium has been used very variously since its coinage by Lankester (1877). It might be well to limit it in the future to tubular excretory organs not containing entoblast. In the descriptive part of the paper I have discussed special homologies of excretory organs within the same group, such as relations of embryonic to adult nephridia, of meganephridia and plectonephridia, homologies of tracheæ, etc.; these need not be repeated here.

ucts, and contain no mesentoblast. I would propose that Hatschek's (1888) term protonephridium be limited to them.

From such protonephridia the other types of nephridia have probably been derived by the persistence of only the discharge ducts, or portions of them, of the former and by the substitution of mesentoblastic elements for their other portions. The only elements of the protonephridia that have been retained, it should be repeated, are their distal nephridiopores with more or less of the connectant discharge ducts, while the remainder of the protonephridia, all the excretory portion proper, has been replaced by mesentoblastic elements. Accordingly, the two other main kinds of nephridia of which we shall have to speak can be at the most compared only in part with these protonephridia, only their distal nephridioporal ends can be so compared. The more specialized kinds of nephridia have probably originated from the protonephridia, not as further specializations of them but rather by addition of extraneous elements; on the whole they are not homologous.

These more specialized nephridia with mesentoblastic constituents fall into two main groups.

The first of them consists of types 8 and 9, both of which have in common the union of an ectoblastic duct with the peritoneum but have no retroperitoneal mesentoblast. They are either urogenital, or are homodynamous with genital ducts (?also in the Enteropneusta). Their main difference is that in type 8 the peritoneal invagination is more pronounced as a rule, and that in type 9 the connectant cœlom has become exclusively excretory. These differences are not important, and these two types are in general homologous. Until retroperitoneal elements are discovered for them they must be considered distinct from the following; and to them the name *cœlonephridium* might be given.

The second kind of the more specialized nephridia comprises types 10 and 11, both characterized by the union of ectoblast with retroperitoneal mesentoblast. Type 11 differs from 10 by the addition of a cœlomostome (peritoneal funnel), in the manner made known particularly by the studies of E. Meyer and Goodrich. Their essential peculiarity is the retroperitoneal mesentoblast, not the peritoneal funnel. Hatschek (1888) classed these together with

the preceding as metanephridia, and diagnosed them by the presence of a cœlomostome; but the difference with regard to the retroperitoneal element seems to me so important that these should be held distinct from the preceding, and in that case it would be well to limit the term metanephridium to types 10 and 11.

The three main kinds of nephridia that these considerations lead us to distinguish may be briefly compared as follows: *Protonephridium* (types 3, 4, 7), wholly ectoblastic or mesectoblastic (possibly in some cases both ectoblastic and mesectoblastic); *cœlonephridium* (types 8, 9), distal ectoblastic portion joining directly with a cœlomostome; *metanephridium* (types 10, 11), distal ectoblastic portion joining with retroperitoneal mesentoblast, and the latter connecting or not connecting with a cœlomostome. Only the second and third of these ever serve as genital ducts or are homodynamous with them. The metanephridium is the most complex because it may consist of as many as three elements, and it contains the smallest amount of the ectoblastic constituent.

The protonephridium in the course of transmutation and division of labor has not become entirely replaced, but it has rather become reduced in amount by the substitution of other elements for certain of its parts. And there have been two paths in this process. By the one, a relatively larger portion of the protonephridium has persisted and a cœlomostome has become directly connected with it, exemplified by the cœlonephridium. By the other a relatively smaller portion of it has maintained itself, to this has been added a secretory tube of retroperitoneal mesentoblastic tissue, and to the latter in some cases a cœlomostome, as illustrated by the metanephridium. The cœlomostome is homologically a genital funnel, as demonstrated by Meyer and Goodrich, comparable with a genital duct of, *e. g.*, a Nemertean. But what the retroperitoneal mesentoblastic element was originally, before it attached itself to a protonephridium, we are unable to decide; it may have originated from the outer layer, that outside of the peritoneum, of a primitive gonadal pouch.

We have now to see how these conclusions relate themselves to the views of other students. It will not be necessary to attempt a full historical review of the various opinions because a good

discussion of them has been recently furnished by Lang (1903). There are two main views: (1) That the nephridia of all the Metazoa are essentially homologous, and (2) that those of the higher Metazoa are dyshomologous with the protonephridia.

The first of these has been maintained particularly by Lang (1881, 1884, 1903). To him the starting point is the condition in the Turbellarian *Gunda,* where there are continuous longitudinal main trunks, and more or less regularly arranged excretory ducts. He holds that such a condition has maintained itself in the case of the plectonephridia of the Hirudinea and Oligochæta, but that it has become modified in other Annelids by the segmentation of the longitudinal trunks. This idea is in a sense a necessary corollary of his view of the close relationship of the Turbellaria and Hirudinea. Besides the similarity in the Turbellaria and the Hirudinea above mentioned, he adduces the following main anatomical resemblances. (1) Hatschek's contention that in *Polygordius* the adult nephridia develop as outgrowths from a continuous longitudinal canal; the error of this observation has since been pointed out by Fraipont, Meyer, and Woltereck. (2) The presence of net-like nephridia (plectonephridia) in the Annelids; I have entered into the question of the homologies of these in the descriptive section upon the Oligochæta, and here need only recall that Vejdovský's embryological studies have shown that the plectonephric condition is secondary, derived from the meganephric. (3) The similarity in histological structure of the two kinds of nephridia. (4) Occurrence of serial provisory larval nephridia in Polychætes, that closely resemble protonephridia; that these are homologous with larval protonephridia as well as with the definitive ones, accordingly, that the protonephridia are homologous with segmental organs. Thus Lang derived (1903) "all the segmental nephridia of the Annelids from the segmental portions of the water vascular system that open externally, on the premise that in the Annelids those canals have not persisted which joined the successive segments of the water vascular system. Such a nephridial segment would have consisted in the ancestors of the Annelids of a pair of water vascular trees with excretory ciliated cells on the terminal ends of the capillary branches, and of a trunk opening outward.

. . . Since in the development of the Annelids the head end of the body precedes and the trunk with its successive segments first later comes to formation, so develops first the first nephridial tree pair, the head kidney adapted to the larval body, whose homology with the water vascular system is not contended even by the opponents of the unit theory, later perhaps a second and possibly still a third similar pair with reduced branching. This most anterior pair of nephridial trees that functions during the earliest larval life, at a time when there is still no secondary body cavity developed in the regions concerned, became in the phylogeny a transitory provisory structure, as can be demonstrated on so many larval organs, while the succeeding nephridial pairs of the trunk segments changed to segmental organs."

The other main view is that represented by Bergh (1885). According to him the larval nephridia of the Cœlomata are homologous with the protonephridia, while the adult nephridia of the Annelids are homologous with the gonadal ducts of the Platodes but not homologous with the protonephridia. Thus he concluded (as Williams did long before) that the segmental organs of Annelids were originally genital ducts and later changed into excretory organs; while the protonephridia do not communicate with the cœlom and never serve as genital ducts.

Goodrich has recently represented a view that in the main supports Lang's. To him there are "nephridia" proper that never serve as genital ducts; he considers all of these ectoblastic invaginations and essentially homologous. Then, adding materially to the discoveries of Eisig and E. Meyer, amplifying them, he find that upon such a nephridium a cœlomostome (peritoneal funnel, genital funnel) may become grafted, giving rise then to a complex "nephromixium." To Goodrich all nephridia are essentially homologous, they differ only in being combined or not combined with a cœlomostome.[15] His argument like Lang's is rather anatomical than embryological. Both of these investigators also lay great stress upon the presence in Annelid nephridia of the solenocytes, cells similar to the flame cells of protonephridia; Goodrich argues that such com-

[15] In the descriptive part under the caption of Polychæta, Goodrich's ideas are given more *in extenso*.

plex cells could not have arisen independently in the two groups, rather that their presence in them means homology of the organs concerned.

It will be seen that my views do not coincide exactly with any of the preceding. I agree entirely with Meyer and Goodrich that the cœlomostome is an organ of origin independent from the nephridium, one that in some cases may connect with the latter. This cœlomostome is equivalent to the genital duct of a lower metazoan, as shown by Bergh. I agree also with Lang that the excretory ducts of the protonephridia have maintained themselves in part in the higher Metazoa, and that the longitudinal canals have disappeared. But I have tried to show that while sometimes such an excretory duct joins directly with a cœlomostome, forming what I call a cœlonephridium, in other cases it joins with retroperitoneal mesentoblastic tissue and the latter may secondarily join with a cœlomostome (metanephridium). In other words, we have to reckon with a retroperitoneal element that frequently forms the greater portion of the nephridium, and this is what Lang and Goodrich have failed to take into account. And I differ from Bergh in concluding that the metanephridium is not in its entirety equivalent to a genital duct, but that only a portion of it (the cœlomostome) is. Goodrich's mistake, if my interpretation is correct, is in assuming that there are only two elements, ectoblastic tube and peritoneal cœlomostome; he entirely neglects the retroperitoneal tissue, and yet this is just what shows the dyshomology of protonephridium and metanephridium. It is a mistake that has resulted from too exclusive reliance upon phenomena of adult structure with neglect of comparative embryology. And the arguments from histological similarity, intracellular cavity, similarity of solenocytes to flame cells, etc., can have little weight now that we are acquainted with still more striking cases of histological convergence as notably the case of the Malpighian vessels of Insects and those of Arachnids. Goodrich has excellently analyzed the history of the cœlomostome and has thereby greatly clarified our knowledge of nephridia. But he has omitted entirely from his general conclusions the retroperitoneal element which has come to supplant the protonephridium

almost entirely thus excluding the homology of the protonephridium and metanephridium.

It will be noted that in my considerations I have entirely excluded the argument from the side of the recapitulation theory, for I have maintained (1906) that this theory is fundamentally erroneous. I have compared corresponding stages, adult or embryonic, of the different groups, have stressed embryological resemblances, but have not compared an adult stage of one organ with an embryonic one of another.

It might be expected that I should now enter upon the question of the phylogenetic significance of the cœlom, because this space has so often a close anatomical connection with nephridia. But I have nothing new to add to the discussion, and for a good representation of it would refer to the treatments by E. Meyer (1901) and Lang (1903). I need only state that there are three main theories in explanation of the origin of the cœlom. The oldest was founded by Sedgwick, and is to the effect that the cœlom is an enterocœlic diverticulum, referable to a gastral pocket of an anthozoan. This has deservedly received little support. Next came the gonocœl theory, foreshadowed by Hatschek, elaborated particularly by Bergh and E. Meyer, and more recently supported by Lang and Goodrich; it concludes that the cœlomic sac of a higher metazoan is the amplified derivative of the genital pouch (gonad) of such a form as a Platode, therefore that the mesentoblast is referable to germ cells The third view is the nephrocœl theory, founded by Faussek (1901) and Ziegler (1898), that the cœlom was originally an excretory organ and that the germ cells have associated themselves secondarily with it. Of these three theories the gonocœl theory seems to me to receive the fullest support from the facts of anatomy and embryology.

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MEDIÆVAL GERMAN SCULPTURE IN THE GERMANIC MUSEUM OF HARVARD UNIVERSITY.

By KUNO FRANCKE.

(*Read April 25, 1908.*)

There is a curious anomaly in the equipment of German universities, an anomaly accounted for partly by the traditional cosmopolitanism of German scholarship, partly by the somewhat belated development of Germany into a united and powerful nation.

Whereas for sudents of classical archæology there is provided in nearly every university of the fatherland a well-planned and systematically arranged museum of casts of Greek sculptures, the student of German history would not find at a single one of these universities any collection which would offer to him a fairly accurate representation of the artistic development of his own country. Even in the German capital with its wealth of ethnological and archæological exhibits from Troas and Pergamon, from Egypt and Assyria, from India and South America, no attempt has as yet been made to bring together, in reproductions, the great artistic landmarks of Germany herself. It has been reserved to an American university to make at least a beginning of such an undertaking, but it is interesting to note that the Germanic Museum of Harvard University could not have achieved whatever success it has had thus far, had it not been for the generous interest bestowed upon it by His Majesty the German Emperor. So that this museum, although established on non-German soil, is after all in its way another symptom of the long strides which modern Germany has made toward national greatness and international influence.

The bulk of the collections of the Germanic Museum at Cambridge is devoted to German sculpture of the Middle Ages and the Renaissance, and particular stress is laid upon a good representation of the thirteenth century.

It is not as generally acknowledged as it should be that the thir-

teenth century marks a truly classic epoch in the development of German plastic act. German sculpture between 1220 and 1250 is fully on a level with the great creations of the lyric and epic poetry of chivalry; and no one who is susceptible to the peculiar beauty of Walther von der Vogelweide's minne-song or is impressed with the heroic figures of the Nibelungenlied, of Kudrun, of Parzival, or Tristan, can fail to observe their affinity of spirit with the plastic monuments of Wechselburg and Freiberg, of Naumburg and Halberstadt, of Bamberg and Strassburg. Here as well as there we find a high degree of refinement and measure; a strenuous insistence on courteous decorum; intense moral earnestness linked to a strange fancifulness of imagination; a curious combination of scrupulous attention to certain conventional forms of dress, gesture, and expression, on the one hand, and a free sweep in the delineation of character, on the other. Here as well as there we find a happy union of the universally human with the distinctively mediæval; a wonderful blending of the ideal human type with the characteristic features of the portrait. As the art of Phidias and Praxiteles is an indispensable supplement to the art of Æschylus and Sophocles, for our understanding of Attic culture in its prime, so these works of German sculpture of the thirteenth century stand to us (or should stand to us) by the side of the great productions of the chivalric poets, as incontrovertible proofs of the free and noble conception of humanity reached by mediæval culture at its height.

A brief review of a few at least of these sculptures may serve to elucidate this statement somewhat more fully.

Among the earliest plastic monuments of the thirteenth century are the pulpit and the Crucifixion group of the Church of Wechselburg in Saxony, executed probably between 1210 and 1220. In both monuments it seems as though the artist was still grappling with the problem of form. In the relief from the front of the pulpit—Christ seated on the throne as Judge of the world, surrounded by the symbols of the Evangelists—mastery of form, classic solemnity, exalted repose have indeed been attained. In the more animated scenes of the side reliefs—the sacrifice of Isaac and the healing of the Jews by the brazen serpent—there is a curious contrast between grandeur and awkwardness, sweetness of feeling and naive natural-

ism. And a similar contrast is found in the Crucifixion group. The figures of Mary and John standing under the Cross, as well as that of Joseph of Arimathea holding out the cup to receive the blood of the Saviour, are remarkable for nobility of outline, depth of feeling, and measured beauty of expression. There is a fine sweep of movement in the two angels on the cross-beam, gentle sadness in the figure of Christ, and a mild tenderness in the attitude of God the Father appearing above. The symbolical figures, however—probably Jewdom and Pagandom—on which John and Mary are standing, are tortuous and forced. Apparently, here is an artist who looks at life about him with a keen, penetrating, and receptive eye, but who at the same time is impelled to subject reality to certain canons of measure and proportion which he has not yet made fully his own.

A decided step in advance is made in the sculptures of the Golden Gate of the Cathedral of Freiberg, likewise in Saxony. In the arrangement of plastic figures, both on the sides of the portal and on the archivolts, French influence is clearly seen. But these plastic figures seem here much more independent of the architectural framework than is common in the French sculptures, *e. g.*, those of Chartres Cathedral, which served as models to the German artist; and the human type and bodily proportions are unmistakably original.

A thoroughly satisfactory interpretation of all the figures, human, animal and fantastic, which cover the sides of the portal, the tympanum and the archivolts, and of the fundamental conception underlying them, has not yet been given, although Anton Springer has done a great deal for the identification of individual personages. Springer thinks that the fundamental conception of the whole is the mystic marriage between Christ and the Church, and that all the scenes and figures of the portal may be interpreted as symbolic of this mystic idea. Simpler and more plausible it seems to me to find in this portal a plastic counterpart to dramatic scenes from the cycle of the Christmas plays, the popularity of which in the thirteenth century is proved, for Germany, by a particularly complete example, the Benediktbeuren Christmas Play. Clearly a scene from the Christmas cycle is the one represented in the tympanum of the portal: the Adoration of the Magi, the three kings approaching from

the left, Mary with the child enthroned in the middle, the archangel Gabriel and Joseph at the right. And no less plausibly than this scene may the eight somewhat under life-size figures which flank both sides of the portal be connected with the subject of the Christmas plays. Prophet and Sibyl scenes were very frequently used as introducing the Nativity play proper, one prophet or Sibyl after another entering to testify to the coming of the Saviour. While retaining most of the names suggested by Springer for these eight figures,—John the Baptist and John the Evangelist, David and Solomon, the Queen of Sheba and Bathseba, David and Aaron,—we may call them collectively witnesses to Christ's Nativity.

As to the plastic representations on the four archivolts encircling the tympanum, they are, to be sure, not taken from any actual scene of a Christmas play; but they are entirely in keeping with the joyous, idyllic character of these plays. On the innermost archivolt, nearest to the Adoration of the Magi, there are at the sides the four archangels, in worshipful attitude; in the middle, the Coronation of Mary by Christ. The next archivolt contains six apostles, three at each side, and in the center Abraham with a soul of the blessed in his lap, while an angel reaches out another soul toward him. The third archivolt shows eight figures of apostles and in the center the dove of the Holy Ghost surrounded by angels. On the outermost archivolt, finally, the resurrection of the flesh is represented by ten figures rising from their graves with manifoldly varying expressions of faith, hope and exultation; while the central group, an angel receiving by either hand a saved soul, fittingly symbolizes the last and highest stage of human redemption. All these sculptures, as well as those of the tympanum and the sides of the portal, are distinguished by a remarkable symmetry and adjustment to architectural demands, and by a wonderful mellowness and purity of form and an exquisite sweetness and serenity of expression, making an artistic whole of extraordinary beauty and perfection.

The climax, however, of North German art of the thirteenth century is reached in the Portrait Statues of Founders and Patrons of Naumburg Cathedral from the west choir of that church, a series of works which may be definitely assigned to the middle of the thirteenth century. These statues, together with that of a young

ecclesiastic from the same church, are a striking refutation of what since Jacob Burckhardt's "Kultur der Renaissance in Italien" has come to be a popular axiom, the assumption, namely, that modern individualism had its origin in the era of the *rinascimento;* they show conclusively that Burckhardt's phrase of "the discovery of the individual" by the great Italians of the quatro-cento is misleading, that, in other words, the Middle Ages themselves contain the germs of modern individualism. There is nothing in the art of the Renaissance which surpasses these Naumburg statues in fulness, distinctness, and vigor of individual life. Every one of these figures is a type by itself, a fully rounded personality. The two pairs of princely husband and wife, one of the men full of power and determination, the other of youthfully sanguine appearance, one of the women broadly smiling, the other, with a gesture full of reserved dignity, drawing her garment to her face; the canoness standing erect, but with slightly inclined head, thoughtfully gazing down upon a book which she supports with one hand while the other turns over its leaves; the princess drawing her mantle about her; the young ecclesiastic with his carefully arranged hair flowing from his tonsure, holding the missal in front of him; the various knights, one looking out from behind his shield, another supporting his left on the shield and shouldering the sword with his right hand, a third resting both shield and sword in front of him on the ground, while with his right hand he gathers his mantle about his neck, others in still different postures and moods,—there is not a figure among them which did not represent a particular individual at a particular moment, and which did not, without losing itself in capricious imitation of accidental trifles, reproduce life as it is. It is impossible in the face of such works of sculpture as these not to feel that they proceeded from artists deeply versed in the study of human character, fully alive to the problems of human conduct, keenly sensitive to impressions of any sort—in other words, fully developed, highly organized, complicated individuals. One feels that here are seen the mature artistic fruits of the great Hohenstaufen epoch—an epoch rent by tremendous conflicts in church and state, and convulsed by the throes of a new intellectual and spiritual birth.

Almost contemporary with these statues, though probably some-

what younger, is the Naumburg Rood Screen separating the west choir of the Cathedral from the nave. The sculptures of this rood screen form an interesting contrast to the sculptures of the Freiberg Golden Gate, analyzed before. While the Freiberg sculptures present a plastic counterpart to the mediæval Christmas plays, we have in the Naumburg rood screen a plastic counterpart to the Passion plays. On the middle beam of the door leading through the screen, which has the shape of a cross, the figure of the dying Saviour is suspended, while on each side of the door there stand in niches the over life-size figures of Mary and John. The other scenes of the Passion, from the Last Supper to the Bearing of the Cross, are brought to view in high reliefs which as a continuous frieze, crowned by a Gothic canopy, give to the whole structure a most impressive attic-like top. These sculptures seem to mark a stage of development somewhat beyond that reached by the Naumburg portrait statues. They are signalized by intense dramatic power. Some of the scenes of the frieze in particular impress one as direct transpositions into stone of scenes from the Passion Play stage. They excel even the portrait statues in freedom and sweep of movement and in keenness of realistic characterization. On the other hand, they show a tendency toward exaggeration, which occasionally (as in John and Mary) leads to a strained and distorted expression of feeling; and, in the portrayal of the vulgar and the commonplace, they occasionally (as in the representatives of the Jewish rabble) diverge into caricature. They are, then, clear anticipations of the ultra-naturalistic, and therefore unnatural tendency of later Gothic sculpture.

We may properly close our review by selecting at least one group of South German sculptures affording a striking example of the strong influence exerted by French Gothic art upon this part of Germany: I mean the "Death of Mary" and the "Ecclesia and Synagoga" from the Romanesque portal of Strassburg Cathedral. The Death of Mary is one of the noblest creations in the whole history of art. The Virgin is represented reclining on a couch, wrapped in a garment which reveals with rare delicacy the lines of her body. Her face is majestic, Juno-like. Although the moment represented is after her death, her eyes are still open and have a

look of heavenly exaltation. Behind her couch, in the middle of the tympanum, stands Christ, holding Mary's soul (in the form of an infant) in his left hand, his right hand raised in blessing. Mary Magdalen cowers in front of the couch, wringing her hands, her face expressing deepest sorrow. The space at the sides and back of the death-bed is filled with the figures of the Disciples, some of them giving way to grief, others contemplative, others transfigured, all of them filled with holy awe and deep religious feeling. The graceful vine which runs along the edge of the Romanesque arch of the tympanum gives to the whole composition a fitting enclosure. In this monument the French sense of form and German feeling seem most happily blended.

Of no less refinement are the statues of Ecclesia and Synagoga. To contrast the Church triumphant and the Synagogue defeated was a very common conception both in the religious sculpture and in the religious drama of the Middle Ages. Noteworthy instances of their occurrence in sculpture are the statues of Rheims Cathedral, the north portal of Bamberg Cathedral, and the vestibule of the Cathedral of Freiburg im Breisgau; of their introduction into the drama, the part played by them in the Ludus de Antichristo and the Alsfeld Play. Of all plastic representations, these Strassburg statues are the most exquisite. The Church, with wide-flowing mantle, the crown on her head, her right hand holding the standard of the cross, her left bearing the communion chalice, stands erect and dignified at the left side of the portal, looking with pride and disdain at her adversary on the opposite side. The Synagogue wears neither crown nor mantle; in her left hand she holds the table of the Mosaic law turned downward, in the right a standard, the shaft of which is broken in many places; her eyes are bandaged (to indicate that she does not see the true light), and her face is turned away from the Church and is bent slightly down. In spite of her humiliation, she appears more human and lovable than her victorious rival. Both figures together are perhaps unsurpassed in mediæval sculpture for grace and delicacy of outline; only in the somewhat coquettish twist of the hips there is observable a slight indication that the highest point in the classic epoch of plastic art

has already been passed and that the age of extravagant emotion and artificiality is setting in.

When, in November, 1903, these and other precious gifts of the German Emperor were temporarily installed in the insignificant little building which Harvard University could spare for them as a scanty shelter, it was hoped that only a short time would elapse before a new and worthy museum building would have been erected through the liberality of American friends of German culture. These hopes have not yet been fulfilled. Here is the opportunity for our fellow citizens of German origin to prove to the world that they do not leave their ideals at home when they leave the fatherland; and here is a chance for all Americans to show their appreciation of what German culture has given to this country.

CAMBRIDGE, MASS.

Stated Meeting October 2, 1908.

Secretary HOLLAND in the Chair.

Dr. E. A. Spitzka, a newly elected member, was presented to the chair and took his seat in the Society.

Letters accepting membership were read from:

Prof. Richard Hawley Tucker.

Prof. Albrecht F. K. Penck.

Prof. Herbert Weir Smyth.

Letters were received

From the City of Faenza inviting the Society to be represented at the Torricelli tercentenary.

From the University of Cambridge inviting the Society to participate in the commemoration of the centenary of Charles Darwin's birth in June, 1909, and Prof. Henry F. Osborn was appointed to represent the Society on the occasion.

From the Physico-Medical Society at Erlangen, thanking the Society for its congratulatory address on the occasion of its centenary celebration.

The decease was announced of:

Hon. Grover Cleveland, at Princeton, N. J., on June 25, 1908, æt. 71.

Prof. F. L. Otto Röhrig, at Pasadena, Cal., on July 14, 1908, æt. 89.

Dr. Ainsworth Rand Spofford, at Holderness, N. H., on August 12, 1908, æt. 83.

Prof. Antoine Henri Becquerel, at Croisic, in Brittany, on August 25, 1908, æt. 56.

Prof. E. Mascart, at Paris, on August 26, 1908, æt. 71.

Prof. Dr. Hugo von Meltzel, of Koloszvar, Hungary.

The following papers were read:

"The Humming Telephone," by Prof. A. E. Kennelly and Walter L. Upson. (See page 329.)

"On the After-images of Subliminally Colored Stimuli," by Edward Bradford Titchener and William Henry Pyle. (See page 366.)

Stated Meeting October 16, 1908.

President KEEN in the Chair.

The decease was announced of President Daniel Coit Gilman, at Norwich, Conn., on October 15, 1908, æt. 77.

Dr. Edward O. Hovey read a paper entitled "A contribution to the History of Mont Pelée, Martinique."

Stated Meeting November 6, 1908.

President KEEN in the Chair.

A letter was received from the Board of Curators and Faculty of the University of Missouri, inviting the Society to be represented at the inauguration of Albert Ross Hill, LL.D., as president of the University, at Columbia, Mo., on December 10 and 11, 1908, and Dr. William Trelease was appointed to represent the Society on the occasion.

The decease was announced of Prof. Otis T. Mason, at Washington, D. C., on November 5, 1908, æt. 70.

Dr. Alexis Carrel read a paper entitled "Recent Studies in Transplantation of Organs in Animals" (see page 677), which was discussed by President Keen, Dr. Coplin, Dr. Eshner and Dr. Carrel.

HEPATOSCOPY AND ASTROLOGY IN BABYLONIA AND ASSYRIA.

By MORRIS JASTROW, Jr.

(*Read December 4, 1908.*)

In any general study of the subject of divination we must distinguish between two forms which for want of a better designation we may distinguish as voluntary and involuntary. Under voluntary divination is meant the act of deliberately seeking out some object or means through which one may hope to pierce the unknown future, hidden from the ordinary gaze. The placing of marked arrows before the image of a deity, and according to the ones drawn by lot, to determine what the god may have in mind or what his pleasure may be is an illustration of voluntary divination as practiced among the ancient Arabs.[1] Sending out birds selected for the purpose and noting the direction and manner of their flight[2] may be instanced as another procedure of direct divination. Among the Babylonians and Assyrians, the common method of voluntary divination was the examination of the liver of the sacrificial animal—invariably for this purpose a sheep—and, according to signs noted in the various parts of that organ, to diagnose the intentions of the gods as the arbiters of human fate and as the powers presiding over all occurrences on earth.

Involuntary divination, on the other hand, rests on the interpretation of all manner of signs and phenomena that without being sought out force themselves on our notice. Preeminent among such signs is the observation of the phenomena of the heavens, primarily the movements and aspects of the sun, moon and planets with the gradual extension to the observation of clouds, of constellations and of single particularly prominent stars—as practiced by the cultural

[1] Wellhausen, "Reste Arabischen Heidenthums," p. 126.
[2] Wissowa, "Religion der Römer," p. 457, note 3.

nations of antiquity.[3] In addition to this branch of involuntary divination, we have the significance attached to diverse occurrences that by their more or less unusual or striking character attract attention or that for any other reason were regarded as fraught with some special importance. The interpretation of dreams falls within this category. Monstrosities among human beings and animals form another subdivision, while peculiar actions among animals—snakes, dogs, ravens, locusts and the like—further extend the scope of involuntary divination until it becomes practically boundless. All the little mishaps and accidents of daily life were looked upon as signs, indicative of the disposition of the gods towards men, and in a still larger sense, as affecting the general welfare, were storms, floods, swollen streams, climatic disturbances and more the like.

In order to differentiate between these two methods of divination we may designate the signs derived from voluntary divination as omens, and those obtained from involuntary divination as portents, while within the field of involuntary divination two broad divisions may be recognized, the one represented by portents connected with the phenomena of the heavens, including clouds, storms and rains, and such as are connected with terrestrial phenomena. In grouping the portents derived from the observation of the phenomena of nature under the general heading of astrology, it must therefore be borne in mind that the term includes more than the mere study of the stars, but so far at least as Babylonia and Assyria are concerned, there is no distinction between the character of the interpretations offered for the phenomena of the heavens in the narrower sense, and such phenomena as are merely associated with the heavens. For the Babylonians and Assyrians, as for the nations of antiquity in general, heaven is not very far removed from the earth.[4] It was supposed to begin where the solid earth came to an end and indeed the tops of mountains so frequently enveloped in clouds appear to have been regarded as bordering on the domain of heaven if not

[3] Dr. J. G. Frazer calls my attention to the fact that astrology in any proper sense is not found among peoples of primitive culture.

[4] This view underlies the Biblical story of the building of the Tower of Babel (Genesis, chapter XI.), as is shown by the circumstance that the task of building a tower which should reach to heaven is not looked upon as an impossible task but as a wicked one.

actually a part of it. Hence to place the seat of the gods on the tops of mountains, as was so frequently done by nations of antiquity, was equivalent to assigning them to the heavens.

Confining ourselves to Babylonia and Assyria, we find that although divination through the interpretation of terrestrial phenomena—dreams, monstrosities, actions of animals, mishaps, swollen streams, etc., etc.—also play a prominent role and that within the field of voluntary divination we have by the side of hepatoscopy (or divination through the liver), other procedures such as the interpretation of the action of oil bubbles in a basin of water,[5] the two chief methods of divination, forming part of the official cult, are Hepatoscopy and Astrology.[6] Both forms were developed into elaborate systems marked by definite rules of interpretation, consistently and logically applied. Extensive collections of omens and portents were compiled by Babylonian and Assyrian priests attached to the temples, in which all signs noted on the liver of sheep and all manner of phenomena observed in connection with sun, moon, planets, constellations and stars on the one hand, and with clouds, storms, rains and floods on the other, were entered together with the interpretation of the signs. The evident endeavor of the compilers was to make the collections as comprehensive as possible so as to provide for all contingencies, since the purpose of the collections was to serve as guides and handbooks for the priests in their practical labors as well as text-books in instructing the pupils of the temple schools. As a consequence, considerable skill and ingenuity were displayed in arranging the omens and portents systematically so as to facilitate their use. On the other hand, while the signs noted were primarily based on actual cases, the theoretical factor enters largely into play. This led to many signs being entered in both classes of divination

[5] See Hunger, "Becherwahrsagung bei den Babyloniern" (Leipzig, 1903).

[6] For details with copious translations of texts see the writer's "Religion Babyloniens und Assyriens," parts 10 to 14, as well as various articles on special points such as "The Signs and Names for the Liver in Babylonian" (*Zeitschrift für Assyriologie*, XX., pp. 105–129); "The Liver in Antiquity and the Beginnings of Anatomy" (*University of Pennsylvania Medical Bulletin*, January, 1908, and Trans. of the Phila. College of Physicians, 3d Series, XXIX., pp. 117–138); "Sign and Name for Planet in Babylonian" (PROCEEDINGS OF THE AMER. PHILOS. SOCIETY, XLVII., pp. 141–156).

which represent such as in the opinion of the priests *might* occur. Certain rules of interpretation having been devised, based on actual occurrences following upon the signs noted, these rules were applied to contingent cases which might occur; and often in astrological texts, signs are even entered which have no practical significance at all but purely a theoretical interest as illustrations of the extremes to which the system of interpretation was pushed.

In the case of both methods the interpretations have reference almost exclusively to the general welfare and not to the individual, to crops, war, pestilence, victory, defeat, famine, plenty, favorable or unfavorable climatic conditions and the like. The individual plays a very minor role, and when he is introduced, in most cases it is the king who is directly mentioned or indirectly referred to. Even the welfare of the king is bound up with the welfare of the country under the view of kingship which continues to hold good till the end of the Babylonian-Assyrian control and according to which the king's welfare, because of his peculiar relationship to the gods, conditions the general prosperity and happiness;[7] and this applies also to signs connected with a member of the royal household. It is because of this bearing of both forms of divination on the general welfare that they form integral parts of the official cult. Especially is this the case with the rites of hepatoscopy which, as texts from the days of the Assyrian empire show, formed part of a regular ritual.[8]

More important, however, than this aspect of hepatoscopy and astrology in Babylonia and Assyria is the circumstance that both methods rest upon a well-defined theory and are therefore not to be viewed as merely arbitrarily chosen devices. In the case of hepatoscopy the underlying theory may be summed up as follows. The sacrificial animal on being accepted by the deity to whom it is offered is assimilated to the deity. The deity becomes one with it, much in the same way as the one who partakes of an animal becomes part of that animal, or the animal part of him. The soul of the animal is thus put in harmonious accord with the soul of the god.

[7] See J. G. Frazer, "Lectures on the Early History of Kingship."

[8] See Jastrow, "Religion Babyloniens und Assyriens," II., pp. 174 seq. and 300 seq.

PROC. AMER. PHIL. SOC. XLVII. 190 PP, PRINTED FEBRUARY 6, 1909.

The two agree as two watches regulated to be in perfect unison. If, therefore, one can read the soul of the animal, one enters at the same time into the inner being of the god. Now according to a view widespread still among people living in a state of primitive culture, the seat of life is in the liver, which is not only the organ of emotional activity but of intellectual functions as well, the source of all emotions high and low, of thought, will and all manifestations of what we ordinarily call soul life.[9] From this point of view the liver is the seat of life and of the soul, as the ancients conceived vitality and its inward and outward phenomena.

The combination of these two conceptions (1) of the liver as the seat of the soul and (2) of the assimilation of the soul of the sacrificial animal to the soul of the deity to whom it is offered and who accepts it, leads to the conclusion that if one is able to read the soul of the animal as revealed in the condition of the liver and of the signs thereon, the soul including, therefore, the will and intention of the deity is revealed. Through the liver of the sacrificial animal one enters as it were into the workshop of the gods. The mind of the god is reflected in the liver of the sacrificial animal like an image in a mirror—to use the figure introduced by Plato in an interesting passage of the Timaeus[10] bearing on divination through the liver.

As for the system of interpretation of the signs noted it revolves largely around a more or less natural association of ideas. The chief parts of the liver to which attention was directed being the right and left lower lobes, the upper lobe with its two appendices, the larger one known as the *processus pyramidalis* and the smaller

[9] For further details regarding this view of the liver which also underlies hepatoscopy among the Etruscans, Greeks and Romans see Jastrow, "Religion Babyloniens und Assyriens," II., pp. 213 seq. In a special article (shortly to be published) on "The Liver as the Seat of the Soul" I have set forth the historical development of the location of the soul in the liver, in the heart and in the head successively. The second stage, though reached by the Babylonians and Assyrians, never found expression in Hepatoscopy, whereas among the Romans from a certain period on, the heart and occasionally the lungs and even the milt were also examined. The third stage was reached too late for incorporation into the divination rites, but in phrenology as an extra-official pseudo-scientific form of divination we have the outward expression of the belief which placed the soul in the brain.

[10] § 71 C.

one as the *processus papillaris,* the gall-bladder, the cystic duct, the hepatic duct, the common bile-duct, the hepatic vein and the "liver gate" (*porta hepatis*). A swollen gall-bladder was interpreted as pointing to an enlargement or increase of power, a long cystic duct to a long reign, a depression in the liver gate to a decrease in power and so forth. Through the further distinction between right and left, the former representing the favorable side, the latter the unfavorable side, the signs in question referred to the king's side or to the enemy's side, as the case might be. Besides the parts of the liver, markings on the liver—holes, lines, and depressions—due largely to the traces on the liver surface of the subsidiary ducts and veins, were accorded a special significance. According to the shape of these markings, frequently fantastically pictured as weapons of the gods, an interpretation, likewise based on association of ideas, was offered and in this way the field of hepatoscopy was further extended. No two livers were ever exactly alike, and it will readily be seen how in the course of time the collections of signs with their interpretation would grow to huge proportions, and the opportunity thus given for the imagination and fancy of the divining priest—the *bârû* or "inspector"[11] as he was called, to roam over a boundless territory. To the credit of the Babylonian and Assyrian priests be it said that so far as the evidence goes, they applied the elaborate and complicated system devised by them logically and consistently. They did not hesitate to announce to the kings an unfavorable result of the examination of the signs. Grouping all the signs noted together, if the unfavorable signs predominated, a second sheep was offered and the liver examined, and if the result of this diagnosis was also unfavorable, the omens were taken for a third time. The frequency with which in official reports to the kings unfavorable prognostications are set forth[12] warrants the con-

[11] The underlying stem is the common term for "to see." The *bârû* as "the seer" was the one who by means of an "inspection" foretold the future. The term was extended also to the "inspector" of the heavens or the astrologer. In Hebrew we have as an equivalent *rô'ēh* and in an article "*Rô'ēh* and *Hôzēh*" (*Journal of Biblical Literature,* Vol. XXVIII., part I) I have tried to show that the *rô'ēh* like the *bârû* was originally an "inspector" of some object through which the future was divined.

[12] Jastrow, *o. c.,* II., p. 287 seq. for examples.

clusion that the diviners were far removed from resorting to deception and to tricky devices such as are reported of augurs among Greeks and Romans.[13] Indeed the mere circumstance that hepatoscopy prevailed uninterruptedly from the earliest to the latest periods, and that on all important occasions it was resorted to as the official means of ascertaining the will and intentions of the gods, is a testimony to the conscientious manner in which the priests must have carried out their tasks.

In passing from hepatoscopy to astrology—the term always used in the larger sense above pointed out[15]—we pass also from the domain of popular and to a large extent primitive beliefs to a domain of speculation that in comparison justly merits the designation scientific. Astrology in Babylonia and Assyria rests on the identification of the heavenly bodies with the gods of the pantheon. While in the case of the personification of the sun and moon as deities we are still within the province of popular and primitive conceptions, we pass beyond this province in the extension of such personification to the planets and stars. It lies in the nature of animism, which is certainly to be regarded as a stage in the development of religious beliefs, even if it is not admitted to be the starting-point of such development, not to distinguish sharply between the manifestation of a personified power and the seat of that power. The sun is at once the sun-god and the seat of that god; and the same applies to the moon. Both, accordingly, have their places in the heavens. Storms, rains, thunder and lightning likewise come from the heavens and hence the gods representing the personification of these powers also have their seats in the heavens. Such conceptions are a direct outcome of popular and primitive methods of thought, and we may perhaps go a step farther and assume that by analogy other powers whose manifestations proceeded from a hidden source were assigned to the heavens, but this step is far removed from the identification of *all* the stars with deities and still farther from projecting

[13] See, *e. g.*, the anecdotes related by Polyænus, "Strategicon," IV., 20, and Frontinus, "Strategematicon," I., XI., 15. Compare also Hippolytus, Refutatio, IV., 40.

[14] The earliest reference occurs in the inscriptions of Gudea (c. 2500 B. C.), the latest in the inscriptions of Nabonidus, the last king of Babylonia. See Jastrow, *o. c.*, II., p. 273 and 247 seq.

[15] See above, p. 647.

the seats of *all* gods and goddesses on to the heavens. Again, the influence of moon and sun, as well as storms with their accompanying phenomena, on the fate, welfare and happiness of mankind was so apparent as to force itself upon the notice even of people living in a state of primitive culture; and when we pass to the higher stages of nomadic, semi-nomadic and agricultural life, the dependence of the country's prosperity and of the individual's welfare upon sun, moon and climatic conditions would be correspondingly increased. The observation of the movements and aspects of sun and moon would follow as a natural consequence, and we may suppose that at a comparatively early stage in cultural development crude and sporadic attempts might be made on the basis of empirical observations to select the favorable moment for such actions as the undertaking of a journey, for hunting or war, for the planting of seeds, for the gathering of the harvest or even for the pairing of domesticated animals. The influence of the planets and stars, however, would be less obvious and indeed until a comparatively advanced stage of intellectual development would not be recognized at all. Astrology in the proper sense, therefore, is not found among peoples of primitive culture[16] who at the most are guided by certain empirical considerations in their enterprises.

The projection of the seats of all the gods on the heavens can only have arisen in people's minds as the outcome of theoretical speculation. This, to be sure, represents merely the extension by analogy of the primitive conception of sun, moon and storms, but an extension which for the very reason that it is neither obvious nor the result of actual experience, lies outside of the range of early thought. The views of Cumont[17] and Boll[18] may, therefore, be unhesitatingly accepted that astrology everywhere represents a *scientific* view of the universe—scientific of course in a relative sense, and in comparison with the conceptions that underlie hepatoscopy or with the significance attached to universal occurrences on earth or to the

[16] See above, p. 647, note 3.

[17] "Les Religions Orientales dans le Paganisme Romain" (Paris, 1907), pp. 197 seq.

[18] "Die Erforschung der antiken Astrologie" (*Neue Jahrbücher für das Klassische Altertum*, I., Abt., Bd. XXI.), p. 108 seq.

mishaps and accidents of daily life. Indeed, one may safely go a step further and set up a contrast between hepatoscopy and astrology corresponding to the difference nowadays between the popular views of the universe which are still so largely controlled by superstitious beliefs and crude speculations—instance the hold that astrology, phrenology, chiromancy, clairovoyance, dreams and belief in the power of ghosts still have upon the masses,—and those held by scientific thinkers. The astrological system of Babylonia and Assyria, which is the earliest known to us, might be described as taking the place in antiquity that in modern times is taken by the "Darwinian" theory of evolution in so far as it is the product of the schools and not of popular conceptions.

It may reasonably be supposed that the recognition of the regular movements of the planets and that within certain periods they pass through a well-defined course as do the sun and moon, was the decisive step which led to the departure from along the lines of popular conceptions. With the planets thus placed on a par with sun and moon, it was a natural sequence to regard them also as gods, or, what amounted to the same thing, as the seats of gods, and to endow them with the power to control occurrences on earth. In the oldest astrological texts, as a matter of fact, we find the five planets already identified with the chief gods of the Babylonian-Assyrian pantheon, Jupiter being known as Marduk, Venus as Ishtar, Saturn as Ninib, Mercury as Nebo and Mars as Nergal.[19] This identification in itself is sufficient to establish the advanced character of the entire astrological lore, for the gods in question, according to the popular conceptions and even in the official cult, stand in no connection with the stars. Marduk, Ninib and Nergal are originally solar deities. Nebo appears originally to have been a water deity,[20] while Ishtar is the earth goddess, the symbol and personification of fertility in general. In thus being identified with the planets, the original character of the deities in question is entirely lost sight of. The identification, therefore, represents a break with popular conceptions and with the traditions that had

[19] Kugler, "Sternkunde und Sterndienst in Babel," I., p. 8 with the corrections on pp. 221 and 286.

[20] Jastrow, *o. c.*, I., p. 118.

gathered around these deities. In view of this, it is clear that in dealing with Babylonian-Assyrian astrology we have to do with the theories of the theologians or priests as the representatives of advanced and abstract thought, and not with popular notions. Moreover, the choice of the deities in question and the order in which they are enumerated when introduced as equivalents of the planets are further indications of the speculative spirit which led to their identification with the planets, and also of the time when this identification took its rise. Jupiter-Marduk is always mentioned first and this precedence is evidently a reflection of the period when Marduk was regarded as the head of the pantheon, *i. e.*, the period after Hammurabi with whom as the unifier of the Euphratean states, the city of Babylon as the capital of the empire assumes the definite position it continued to hold till the destruction of the neo-Babylonian kingdom by Cyrus in 539 B. C. The pantheon as constituted during or after the days of Hammurabi assigns to Marduk as the patron deity of Babylon the first position. Marduk takes the place held by Enlil of Nippur and subsequently, as would appear, by Ninib.[21] The other great gods of the pantheon, as found in the Hammurabi period, are precisely the ones identified with the remaining four planets, Ishtar, Ninib, Nebo and Nergal together with Sin the moon-god, Shamash the sun-god and Adad-Ramman the storm-god. The basis upon which Babylonian-Assyrian astrology rests thus assumes the definite formation of a pantheon and moreover the particular form of the pantheon that marks the Hammurabi period, *i. e.*, after 2000 B. C. This does not necessarily mean that astrology dates in Babylonia from this period, for it is possible that there was an earlier series of identification of gods with planets, but that the astrological texts known to us do not revert to originals older than the days of Hammurabi. There are indeed references in the inscriptions of Gudea which would point to the practice of interpreting the signs of the heavens at this earlier period[22] and it may well be therefore that the priests long before Hammurabi had started on the course of speculation which culminated in placing the seats of *all* the gods in the starry firmament. But whatever the age of Babylonian-Assyrian

[21] See Jastrow, *o. c.*, I., p. 452 seq.
[22] See Jastrow, *o. c.*, II., p. 423.

astrology may be, it must have involved the dissociation of the gods identified with planets and stars from their original character as solar, agricultural, water or chthonic deities, and it is also reasonable to assume that it is subsequent to the period when, by a process of selection, certain deities, though originally local in character, were differentiated from the many other local gods and became members of a definitely constituted pantheon consisting of a limited number of great gods and of a larger number of minor deities.

Before passing on to another phase of the subject, it may be proper to point out the more specific factors involved in the identification of the planets with certain gods—all confirmatory of the general thesis that astrology represents a system devised in the schools, and that its very artificial character is indicative of its being a "scientific" and not a "popular" product. Marduk was identified with Jupiter by the natural association which led to assigning the head of the pantheon to the most striking of the planets known to the ancients.[23] In the case of Venus it was probably her double character as morning and evening star that suggested the identification with Ishtar, who as the goddess of fertility likewise presents two aspects in the two divisions of the year—the producer of life and vegetation in the spring and summer, and the one who withdraws her favors in the fall and winter.[24] The dark-red color of Mars appears to have been the factor which prompted the identification with Nergal, the god of the burning summer solstice, of pestilence and death. Nebo becoming in the pantheon of Hammurabi the son of Marduk,[25] a natural association of ideas would lead to assigning him to the smallest of the planets. There would

[23] See Kugler, *o. c.*, p. 14, note 1.

[24] This double character of Ishtar underlies the famous myth commonly known as Ishtar's descent into the lower regions. See Jensen, "Keilinschriftliche Bibliothek," VI., 1, pp. 80–91. The destructive character of Ishtar appears also in the myth of the slaying of Tammuz and in the other capacity of Ishtar as a goddess of war. See Jastrow, *o. c.*, I., pp. 82 seq.

[25] See Jastrow, *o. c.*, I., p. 120. As a concession to the predominance of the Nebo cult in the days of the neo-Babylonian dynasty, we find in the astronomical texts of the latest period (after 400 B. C.) a change in the order of the planets, Nebo-Mercury assuming the third place, *i. e.*, after Marduk and Ishtar, instead of Ninib-Saturn who is assigned to the fourth place. See Kugler, *o. c.*, p. 13.

thus remain for Ninib the planet Saturn whose large size would have been regarded as appropriate for a solar deity once occupying the position that afterwards was assumed by Marduk.

The planets thus representing the great gods of the pantheon, the prominent fixed stars were associated with the minor deities and while in the case of many of the stars occurring in the purely astronomical texts which belong to the later and latest periods of Babylonian culture,[26] no definite association with specific deities was worked out, yet it is to be borne in mind that all the stars were regarded as gods in a logical and consistent extension of the principle which gave rise to astrology as a system of divination. It is one of the many merits of Hugo Winckler[27] to have demonstrated as one of the tenets of the Babylonian-Assyrian conception of the universe a perfect correspondence between occurrences on earth and phenomena in heaven.[27a] Earth and heaven stand related to each other as a reflection in a mirror to the original which is reflected. Since all that happens is due to the gods, it follows from the speculative view which places the gods in the heavens that occurrences on earth are prepared in the heavens. What one sees in the heavens is therefore the activity of the gods preparing the events on earth. The constantly changing aspect of the starry universe thus finds a natural explanation. The movements of sun, moon and planets as well as the ever-varying aspects of clouds and all other phenomena of a striking character were the external symptoms of the never-

[26] See Kugler, "Sternkunde," p. 2 and elsewhere whose views have been accepted by Boll, Eduard Meyer, Schmidt and many others. See Jastrow, II., p. 432, note 1, where I have set forth my own position on the important question as to the age of astronomy in Babylonia and Assyria with an endeavor to do justice to both sides of the burning problem.

[27] "Himmels und Weltenbild der Babylonier" (Leipzig, 1893, 2te Auflage) and numerous other monographs of this scholar. See Jastrow, *o. c.*, II., p. 418, note 2.

[27a] The same view prevails among the Indians of Mexico according to Preuss "Die Astralreligion in Mexico in vorspanischer Zeit und in der Gegenwart" (Transactions of the 3d International Congress for the History of Religions I., p. 36 seq.). It is to be noted that also among the Mexican Indians the astral cult included the worship of storm and rain deities (*l. c.*, p. 38 seq.). Preuss is mistaken, however, in regarding this astral religion as "primitive." On the contrary, it betrays all the earmarks of a cult devised by priests on the basis of elaborate cosmical speculations.

ceasing divine activity. The theory of the correspondence between heaven and earth was carried by the theologians of the Euphrates Valley to its logical consequences. Myths and legends were so shaped under the influence of the theory as to admit of a double interpretation, the one having reference to the movements and aspects of the heavenly bodies, the other to occurrences whose scene is placed on earth. A series of acts of creation on earth is counterbalanced by a corresponding series in the heavens.[28] The heavens were divided off into districts with mountains, rivers and cities corresponding to those on earth. The famous Gilgamesh Epic—a composite tale with almost equal proportions of nature myth, legendary lore and dimned historical traditions—admits likewise of a double interpretation, the scenes applying equally to the movements of heavenly bodies and to events on this globe;[28a] and the same holds good for such tales as the story of Etana and the Adapa myth which, besides betraying the work of theological schools in making the tales the medium of conveying doctrinal teaching,[29] are so constructed as to conform with the fundamental principle of a correspondence between heaven and earth.

Corresponding, therefore, to the theory underlying Babylonian-Assyrian hepatoscopy as above set forth, we have in the case of astrology likewise a theory which lifts the endeavor to divine the future through the observation of the planets and stars beyond mere caprice and arbitrary guesswork. Granted the underlying assumption that there is a perfect correspondence between heaven and earth, it follows that if one can grasp the meaning of the aspects and movements of the heavenly bodies one can recognize clearly what the gods are doing, and hence what the future is to be, which, since it is in the hands of the gods, is merely the outcome of their activity as revealed in the heavens. Astrology is, therefore, like hepatoscopy a means of entering into the workshop of the divine

[28] See Zimmern, "Biblische und Babylonische Urgeschichte" (3^te^ Auflage, Leipzig, 1903).

[28a] See Kugler, die Sternenfahrt des Gilgamesch (Stimmen aus Maria-Laach, 1904. Heft. 4).

[29] See Jastrow, "Religion of Babylonia and Assyria" (Boston, 1898), pp. 519–555, and in greater detail in the writer's next volume. "Temples, Myths and Cults of Babylonia and Assyria."

will and intention. Through the planets and stars or rather in the planets and stars one sees the gods at work and if one knows what they are contriving, one knows what occurrences will take place on earth. Again, as in the case of hepatoscopy, past experience and association of ideas are the two main factors involved in the system of interpretation gradually devised by the Babylonian-Assyrian *bârû* priests or "inspectors" in their capacity as astrologers or "inspectors" of the heavens. A favorable event or a favorable outcome of a crisis following upon certain aspects of the heavenly bodies would be made the basis of a favorable prognostication on another occasion when the same conditions presented themselves; and the prognostication would be made without reference to the particular event following upon the original observation. It was not the event that was of importance but merely the circumstance whether it was favorable or unfavorable. On the basis of this experience phenomena were entered as pointing to favorable or unfavorable occurrences, and these entries served as a guide to the priests in the task imposed upon them of divining the future. But while the principle of *post hoc propter hoc* entered largely into the formation of collections of astrological omens—as it did in the collections of hepatoscopical omens[30]—the natural or artificial association of ideas was even a more prominent factor. Normal conditions as a rule were interpreted as favorable. Thus, if the moon and sun appeared in conjunction at the proper time, a favorable prognostication was indicated. If the conjunction took place at a time earlier or later than the expected moment it forboded disaster of some kind. Again, by a perfectly logical association, in case the new moon was seen on the first day of the month, *i. e.*, was not obscured by clouds, the omen was of a favorable character; if, however, clouds obscured it so that the new moon was not visible, difficulties of some kind might be expected. Days were entered as favorable or unfavorable according to these and numerous other indications and though in the case of a specific inquiry of the gods recourse was had to hepatoscopy in order to ascertain what a deity had in mind with regard to the particular situation in question, the signs

[30] See Jastrow, "Religion Babyloniens und Assyriens," II., p. 251 seq., for examples.

involuntarily forced on one's notice by conditions prevailing in the heavens were not and could not be neglected. A few examples from astrological texts will suffice for our purposes. Thus we read in an official report of the Assyrian period:[31]

"If the moon is seen on the first day, good faith and stable conditions in the land. If the first day is abnormally long, the king will have a long reign."

The prognostication is clearly based on a natural association of ideas. From the fact that the new moon is visible on the day set for it, the conclusion is drawn that as the moon kept good faith, as it were, so the king may expect those entrusted with any mission to be faithful and that his subjects in general will be loyal. By a still clearer association long days point to a long reign.

Another report states:[32]

"If the moon is seen out of the expected time, prices will be low.[33] The moon was seen with the sun on the twelfth day. If moon and sun are seen together at an abnormal time, a strong enemy will oppress the land, but the king of Babylonia will accomplish the overthrow of his enemy."

The normal period when moon and sun should be seen at the same time in the heavens is on the fifteenth day—the moment of opposition. The *bârû*-priest reports, however, that the appearance of moon and sun took place already on the twelfth day—earlier, therefore, than was expected. The abnormal condition points to some misfortune and two omens that are to be regarded as extracts from actual collections are introduced, the one referring to economic conditions, the other to political affairs, and though both are unfavorable, yet in the second instance it is added that ultimately the enemy will be overthrown. In the case of such specific prognostications we are perhaps justified in concluding that they rest on past experience. In other words, on some occasion when sun and moon were seen together in the heavens earlier than the fourteenth or fifteenth day of the month, prices went down or an enemy entered the land but was eventually vanquished. The occurrences were

[31] Thompson, "Reports of the Magicians and Astrologers of Nineveh and Babylon" (London, 1900), Vol. I., No. 1.

[32] *o. c.*, No. 119.

[33] Low prices were regarded as an unfavorable condition in Babylonia and Assyria.

accordingly entered as unfavorable in the collections, and when the same conditions again took place, the fact was reported to the king who would thus be warned either against undertaking an expedition or at least would be prepared for some disaster or discomfiture.

To even partially enumerate the phenomena noted in the astrological collections would carry us too far, and it will easily be seen how in the course of time the collections would grow to huge proportions.[34] Halos around the moon or sun, moon and sun eclipses, thunder in certain months or on certain days, one planet or the other standing within the halo around the moon, the appearance of Venus or some other planet at the heliacal rising or at some other point in its course, the appearance of the moon's horns or crescent, the position or appearance of a certain planet or of a certain star are among the phenomena entered and here the prognostications vary according to the season of the year, according to the month or day of the month.[35]

Without losing sight of the purely artificial character of the system of interpretation devised by the Babylonian theologians, one should not withhold one's meed of praise for the consistency with which the elaborate system was carried out for a long stretch of centuries, as well as for the patience displayed in the compilation of the extensive collections of omens of which only portions have come down to us. Moreover, the Babylonian-Assyrian astrology shows that even a superstition can harbor an exalted idea, for the result of the continuous observation of the movements and aspects of planets and stars must have been to impress at all events the priests with the realization of the reign of law in the universe; and it is, assuredly, a decided gain to realize that even the activity of the gods is under the sway of a fixed order. In striking contrast to hepatoscopy which rests upon the arbitrary nature of the gods and merely aims to fathom their caprice, astrology starts with the recognition of the

[34] The best known of such astrological collections in Ashurbanapal's famous library is a series known from the opening words as "When Anu and Enlil" and comprising more than seventy tablets. See Jastrow, *o. c.*, II., p. 424, notes 3 and 4, and copious examples beginning p. 458.

[35] In their ambition to make the collections as complete as possible, the *bârû*-priests even enter phenomena that never occurred, and some that never could have occurred.

fact that the gods as represented by the planets and stars act in concert. The phenomena of the heavens suggest *united* action in place of individual caprice, and the general regularity of the movements of heavenly bodies must soon have suggested to the priests the view that divine government of the universe rests at least to a large extent upon law and order. We may properly assume that this aspect of astrology by which, through constant observation, the permanent impression of awe and reverence for the grandeur of heavenly phenomena was deepened, was an important factor in maintaining the faith in the stars as manifestations of the divine will and of the intentions of the gods towards mankind. The Babylonian *bârû*-priest could reëcho the sentiment of the Psalmist (19, 1–2) who, carried away by the sight that greeted him in the heavens, exclaimed, "The heavens declare the glory of God and the firmanent sheweth his handywork. Day unto day uttereth speech and night unto night sheweth knowledge." To the *bârû*-priest the heavens spoke by day and night, and it was his privilege to interpret to others the knowledge revealed to him.

Attention has already been directed[30] to the fact that in the case of both hepatoscopy and astrology the interpretations of the omens have reference exclusively to the public welfare, to the condition of the crops, to pestilence, to war or victory and that the introduction of the king likewise falls within this category. More than this, the interpretations in both systems are substantially the same, so that a dependence of one system upon the other becomes at least a probable hypothesis. A detailed study of the two systems leads indeed to a confirmation of this thesis and since hepatoscopy, as has been shown, is an outcome of popular conceptions and exists in full force in the earliest period of Babylonian history, it is reasonable to suppose that it was the first to be developed and that the astrological system represents an adaptation of the principles underlying the interpretation of signs on the liver to signs noted in the heavenly bodies. The "scientific" view of the universe that is closely bound up in the astrological system represents, as is obvious, a later stage in cultural development than the "popular" conception upon which hepatoscopy rests. In

[30] See above, p. 649.

the name given to the planets in Babylonia we have, I venture to think, a direct proof of this dependence of astrology upon hepatoscopy. It has always been a puzzle to scholars that the common designation for planet should have been a compound ideograph,[37] the two elements of which signify "sheep" and "dead." Attempts to furnish a satisfactory explanation have failed and the interpretation offered by Babylonian scribes as "causing the death of cattle,"[38] while confirming the division of the sign into the two elements in question, is purely fanciful and is of value chiefly as showing that the real origin of the designation had already in ancient times become obscured. Through a syllabary (II. Rawlinson, Pl. 6, 4 c–d) we learn that the compound sign (Lu-Bat) is to be read *bi-ib-bu* and the context in which the word occurs[39] is sufficient to show that it is one of the names for "sheep." This, moreover, is confirmed by the fact that the first element, Lu, with or without the addition of the sign for "male" designates the "sheep." Now, the second element (Bat) has also the force of *têrtu*, "omen,"[40] the explanation

[37] Lu-Bat. For a full discussion see a special article by the writer "The Sign and Name for Planet in Babylonian" in the PROCEEDINGS OF THE AMERICAN PHILOSOPHICAL SOCIETY, Vol. XLVII., pp. 141–155. It is also to be noted that while all the planets are designated as Lu-Bat or *bibbu*, there are two, Mercury and Saturn, to whom the designation is specially applied. On the reason for this as well as for the explanation of the Babylonian names for Mercury (Lu-Bat Gu-Ud) and Saturn (Lu-Bat Sag-Uš) see the article just referred to, in which on p. 142 a reference should have been added to Zimmern, "Keilinschriften u. das alte Testament," p. 622, seq.

[38] *muš-mit bu-lim* (V. Rawlinson, Pl. 46, Nr. 1 (rev.), 41), in which equation Lu is entered as the equivalent of *bulu* "cattle" and Bat as III., 1 of *mâtu* "cause the death" or "kill." The artifical character of the explanation is revealed by the unwarranted extension of Lu in the general sense of "cattle," nor can Bat without some further qualifying prefix mean "cause to die" but merely "to die" or "to be dead." Lu-Bat could have the force of "sheep that is dead" or "sheep that is killed," but never "sheep (or 'cattle') that kill."

[39] It is followed by *a-tu-du* "goat" and *sap-pa-ru* "mountain goat." Note also that l. 1, a-b Lu = *kir-ru*—a common term for "lamb." Dr. Rudolf Eisler finds in the double sense of the Semitic stem *âmâr* "word" and "sheep" a further support for the thesis here set forth ("Origin of the Eucharist," p. 10—an address before the Third International Congress for the History of Religions at Oxford, Sept. 18, 1908.)

[40] See II., Rawlinson, Pl. 27, No. 2, 46 obv. c-d. Ur-Bat = *ter-tum ša ha-se-e, i. e.*, "omen of the liver," the first element (Ur) being the common

for which is to be sought in the circumstance that through the sacrificial animal, killed for the purpose, an omen was secured. The combination Lu-Bat, "dead sheep," is therefore intended to convey the notion of a "sacrificial sheep," offered to the deity as a means of securing an "omen." So prominent is the part played by hepatoscopy in the Babylonian-Assyrian religion as shown not merely by the extensive omen texts, dealing specifically with divination through the liver,[41] but by the frequent allusions to the rite in historical inscriptions that one is tempted to set up the thesis that the original purpose of sacrifice among the inhabitants of the Euphrates Valley was to ascertain through the sacrificial animal what the future had in store or what the gods had in mind,—this purpose taking precedence of other views of sacrifice such as tribute or alliance with the deity.[42] However this may be, the animal, so far as the evidence goes, invariably chosen for purposes of divination was the "sheep,"[43] and there is one instance[44] in which the combination Lu and Bat occurs in a "liver" divination text to designate the "sacrificial sheep" the liver of which is to be examined as a means of divination. It is with this use of the term that I propose to connect the designation Lu-Bat for "planet." The sheep being the common animal of divination, the term acquired the general force of an "omen" precisely as in Latin we have *auspicium*, originally an augury through "bird observation," *i. e.*, the noting of the flight of birds, becoming the generic term for any kind of an augury, because of the prominence of "bird observation" as a means of divination. Still

ideograph for "liver" (see Jastrow, "Signs and Names for the Liver in Babylonian," in *Zeits. für Assyr.*, XX., p. 105, seq. and p. 127) and the combination thus having the force of "liver omen." The association leading from "dead" to "omen" thus becomes intelligible, since the "dead" or "sacrificed" animal is the medium for procuring an omen.

[41] Over 1,000 of the circa 30,000 fragments of the royal Library of Ninevah are "liver" divination texts. See Jastrow, "Religion Babyloniens und Assyriens," II., p. 211, note 1, and p. 222, note 2.

[42] See Jastrow, *o. c.*, II., p. 217.

[43] So, *e. g.*, in the case of the official reports to Assyrian Kings, in the prayers connected with the divination rite as well as in the omen collections. See Jastrow, *o. c.*, II., pp. 281, 289, 301, 307, 308, etc.; "Cun. Texts," XX., Pl. 1, 1; Boissier, "Documents assyriens relatifs aux Présages," p. 97, 11.

[44] Boissier, *l. c.*, p. 212, 27. Lu(Nita) Bat (u) = *immêru mîtu*.

more striking is the analogy offered by the usage in Greek where the word for bird, ὄρνις or οἰωνός, has acquired the force of "omen."[45] The planets, accordingly, were called "sheep" because the purpose for which they were observed was to serve as "omens," and this view is confirmed by a statement of Diodorus (Bibl. Hist. II., 30) that the Babylonians (or "Chaldeans" as he calls them) called the planets ἡρμενεῖς, "interpreters," because "they reveal (or "interpret) the intention of the gods to men." The term used by Diodorus accurately reproduces the force of Lu-Bat in the sense of an "omen" or "interpretation" of the will and purpose of the gods. If this explanation be admitted, we would thus have a direct evidence of the dependence of astrology upon hepatoscopy, in accord with the reasonable assumption on *a priori* grounds of the rise of astrology subsequent to hepatoscopy. The justification for thus assuming a bond uniting astrology and hepatoscopy is furnished by the evidence for an analogous condition among the Etruscans whose method of hepatoscopy has many points in common with the Babylonian-Assyrian rite.[46] On the famous bronze model of a liver found near Piacenza[47] and which, dating from about the third century B. C., was used as an object lesson for instruction in hepatoscopy, precisely as the clay model of a liver dating from the Hammurabi period was used in a Babylonian temple school,[48] we find the edge of the liver divided into sixteen regions with the names of the deities inhabiting them, corresponding to divisions of the heavens in which the gods have their seats, while on the reverse side there is a line dividing

[45] See the passage in the Birds of Aristophanes ll. 719–22 to which my colleague Prof. Lamberton directed my attention and Xenophon, Anabasis, III., 2, 9, which Dr. R. G. Kent, of the University of Pennsylvania, kindly pointed out to me.

[46] See Thulin, "Die Etruskische Disciplin," I. (Göteborg, 1905), p. xii, seq.

[47] It is sufficient for our purposes to refer to two recent treatises on this remarkable object (a) Thulin, "die Götter des Martianus Capella und der Bronzeleber von Piacenza" (Giessen, 1906), and Körte, "die Bronzeleber von Piacenza," in *Mitt. d. Kais. Deutsch. Arch. Instituts* (Römische Abteilung), XX., pp. 349–379.

[48] Published in "Cun. Texts," VI., Pls. 1 and 2 (with photograph). See Boissier's first attempt at an interpretation, "Note sur un Monument babylonien se rapportant à l'Extispicine" (Genève, 1899). I hope ere long to publish the results of my study of the inscription on this object.

[49] See Körte, *l. c.*, p. 356.

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the liver into "day" and "night."[49] Professor Körte, in a study of this remarkable object, summing up the results of many years of research, explains this by showing that the liver was regarded as a microcosm reflecting the macrocosm,[50] or, in other words, the liver of the sacrificial animal from being originally a reflection of the soul or mind of the god to whom the animal was offered, was brought into connection with the observation of the heavenly bodies revealing the intention of the gods acting in concert. This combination of hepatoscopy with astrology likewise points to the latter system of divination as the later one, dependent in some measure upon the earlier method of divining through the liver.

This leads us to the last two points to be considered here, the relationship of Babylonian-Assyrian astrology to astronomy and the spread of astrology from the Euphrates Valley to other peoples. While astrology even in its most primitive phases assumes some knowledge of astronomy, it stands to reason that since the sole purpose for which the planets and stars were observed was as a means of securing omens, there could be no genuine interest in astronomical lore, pure and simple. As the scope of astrology increased, more stars were added to the field of observation, with each succeeding ages further details of the movements of the planets were noted, and groups of stars were combined into constellations of a more or less fanciful character. It became necessary for purposes of instruction in astrology to systematize and synthesize the knowledge thus acquired from empirical observation. In the course of time a considerable body of "school" literature thus took shape in the form of lists of stars, with attempts to locate them and to set forth some of the phenomena connected with them.[51] For the practical purpose of regulating the calendar further pedagogical aids were devised, and

[50] Körte (p. 362) expresses himself as follows "Die Leber, der Sitz des Lebens nach antiker Auffassung, erscheint als ein Abbild des Weltganzen im kleinen. Wie dieses ist sie in eine rechte und in eine linke Hälfte, eine Tages—und Nachtseite geteilt. Die Trennungslinie entspricht der Ost-Westlinie des Weltalls. Wie das Himmelsgewölbe ist ihr Rand in 16 Regionen geteilt, in denen Götter walten und Zeichen geben können."

[51] As examples of such lists see II. Rawlinson, Pl. 49, Nos. 1, 3, 4; III. Rawlinson, Pl. 57, No. 6, and the texts entered in the Index to Bezold's "Catalogue of the Cuneiform Tablets of the Kouyunjik Collection," p. 2096. These lists in the royal library of Nineveh revert to older Babylonian originals.

thus at a comparatively early age the seeds for a genuine science of astronomy were planted. The fact, however, is significant that, with perhaps some exceptions, we have in the library of Ashurbanapal, representing to a large extent copies from older originals, no texts that can properly be called astronomical.[52] For this reason a reaction has set in among Assyriologists against the view formerly held that astronomy was cultivated at an early period in Babylonia and Assyria.[53] It is certainly significant that the astronomical tablets so far found belong to the latest period and in fact to the age following upon the fall of the Babylonian empire.[54] While we must be warned against pressing the argument *ex silentio* too far, still there is sufficient evidence to warrant the conclusion that the most glorious period of Babylonian astronomy falls in the fourth to the second centuries before this era, that is to say, within the period of the Greek occupation of the Euphrates Valley. According to Kugler,[55] the oldest dated genuinely astronomical tablet belongs to the seventh year of Cambyses, *i. e.*, 522 B. C., although it shows evidence of having been revised on the basis of an older original. We also find evidence of changes both in the astronomical terminology and in the order of the planets after c. 400 B. C.,[56] so that while we are justified in going back to the neo-Babylonian dynasty as the point of departure for the beginnings of a genuine astronomical science, it would be rash to go much farther back than this. At all events,

[52] K. 9794 appears to be purely astronomical. See Bezold, *o. c.*, Vol. V., p. xxv. and iii., p. 1039; also Jeremias, "das Alter der babylonischen Astronomie" (Leipzig, 1908), p. 21.

[53] For a fuller discussion of the recent literature on the subject see Jastrow, *o, c.*, II., pp. 232–434. Kugler, in "Kulturhistorische Bedeutung der Babylonischen Astronomie" (*Vereinsschriften der Görres-Gesellschaft*, 1907, III., pp. 38–50), maintains the late origin of Babylonian astronomy. His views have been accepted by Boll, "die Erforschung der Antiken Astrologie" in *Neue Jahrbücher für das Klassische Altertum*, 1. Abteilung, Bd. XXI., pp. 103–126) and others, while Jeremias ("das Alter der babylonischen Astronomie") and the adherents of the Winckler school cling to the view that astronomy took its rise in the early period of Babylonian history. For a general summary of our present knowledge of Babylonian astronomy, on the basis chiefly of Kugler's researches, see the two articles by Schiaparelli in the *Rivista di Scienza*, III., pp. 213–259, and IV., pp. 24–54.

[54] See Kugler, "Sternkunde und Sterndienst in Babel," I., p. 2.

[55] Sternkunde, p. 61.

[56] *o. c.*, pp. 12, 13, 22, 62, etc.

it is not until we reach the days of the Seleucidian and Arsacidian dynasties that we find astronomical calculations of the movements and of the position of the moon and planets in full swing.

It can hardly be regarded as accidental that the flourishing period of Babylonian astronomy should thus be coincident with the time when, according to definite evidence, Babylonian astrology passed over into Greece. "The conquest of Alexander," as Bouché-Leclercq tersely puts it, "threw down the barriers hitherto separating races and civilizations."[57] To Berosus, the "Chaldaean" priest who wrote in Greek a history of Babylonia and Assyria, the Greeks themselves ascribe the introduction of astrology into their midst. Settling in the island of Cos, the home of Hippocrates, Berosus himself taught the Babylonian system to the students whom the fame of the great physician had attracted to that place.[58] The fragments preserved of the writings of Berosus,[59] few as they are, suffice to show that he gathered his material direct from the sources, and there is therefore no reason to question that he followed conscientiously the methods laid down in the Babylonian collections of astrological omens. While it is of course possible and indeed probable that through the contact with the Persians the Greeks may have heard of the Babylonian system of divining the future through the stars, it is certain that astrology did not take a definite hold on the Greeks and become part of their intellectual outfit until the days of Berosus, *i. e.*, till about the beginning of the third century B. C. A few centuries sufficed to transform Babylonian astrology under the influence of the Greek spirit from the character of an "oriental religion" which as Bouché-Leclercq[60] recognized it had at the time of its adoption, into the appearance of a science. Already advanced students of astronomy, the Greek physicists combined astrology with the principles and speculations of mathematics and brought it into accord with the current systems of philosophy until it became a genuine expression of the Greek spirit and an integral part of Greek culture. A feature which the Greeks introduced and which

[57] L'Astrologie Grecque," p. 35.

[58] Vitruvius, de Architectura, IX., 6. See also Bouché-Leclercq, *o. c.*, pp. 2 and 37.

[59] Cory, "Ancient Fragments," pp. 51–69.

[60] *o. c.*, p. 1.

of itself served to change the aspect of the Babylonian system was the perfection of a method whereby the fate of the individual was brought into connection with the stars. The science of genethlialogy[61] or the casting of the individual horoscope from the position of the stars at the time of an individual's birth is a *distinctly* Greek contribution. The insignificant role that the individual plays in all phases of divination, except in the case of the accidents and unusual incidents that happen to him and which were therefore looked upon as signs sent by the gods to the individual as such, prevented the rise of the thought that the activity of the gods as shown in the heavens had any bearing on the fate of the individual. As we have seen, astrology, just as hepatoscopy, concerned itself in Babylonia and Assyria with the general welfare and the public state. There was no place in either of the two great systems of divination for the individual and we may go a step farther and assert that it was contrary to the entire spirit of the Babylonian-Assyrian religion to suppose that the gods concerned themselves with the individual sufficiently to give him as such, through the stars or through the liver of a sacrificial animal, an indication of what they purposed doing.[62] It was different in Greece where long before the time that Babylonian astrology was assimilated to Greek culture, the individual had asserted himself to an extent undreamed of in the Euphrates Valley. Instead of an intellectual oligarchy with all learning confined to priestly circles, corresponding to the concentration of all political power in the hands of a few privileged families, we have in Greece a republic of letters with an independence of thought only surpassed by the strength of individualism in the political sphere. Religion had long ceased to be the controlling factor or at least the predominant

[61] Bouché Leclercq, *l. c.*, p. 49, while noting that there is no trace of the application of the astrology to the individual horoscope in cuneiform texts, is disposed to attribute this to the dearth of material. Since he wrote his great work that material has largely increased, and it is perfectly safe to conclude that this phase of astrology *never* existed in the Euphrates Valley.

[62] If in a few very late texts (cf. Bouché-Leclercq, *l. c.*, p. 50) we find entries of the birth of a child with the mention of the aspect of the moon, planets and constellations, this is to be ascribed to Greek influence as Bouché-Leclercq himself suggests. Some Greek astrologers even went so far, according to Vitruvius (*l. c.*), as to cast the horoscope of an individual from the time of conception.

factor in Greek civilization. One science after the other had freed itself from the thraldom of religious tradition and, accordingly, astrology, when introduced into Greece, did not become a part of the Greek religion but an element of Greek *science*. Passing on to the Romans[63] as an integral part of Greek culture, and becoming with the spread of Roman authority the general possession of the ancient world, astrology, because of its indissoluble association with astronomy, mathematics, and the philosophical systems of Greece, became part of the heritage of Greece to the world and took on in time the aspects of a religious cult.[63a] With the revival of Greek influence through the intellectual movement following upon the rise and spread of Islamism, astrology took a firm hold on the choice minds of mediaeval Europe by the side of such a force as Aristotelianism,[64] and continued to sway men's minds till the threshold of modern scientific thought, when it was swept away with so many other cherished traditions from the broad highway of science into the byways where it still flourishes at the present time and will no doubt continue to do so for a long time to come. Though somewhat more complicated in its processes, mediaeval and modern astrology is practically identical with the form it took on in Greece.[65] Not only did Greek astrology make its way throughout the West but it spread also to the East, for it has been definitely ascertained that what we find of it in India and even in China is due to the spread of the sphere of Greek influence;[66] and the same holds good for Egypt, where it begins to flourish with the rise of Hellenistic culture.[67]

[63] Bouché-Leclercq, *l. c.*, Chap. XVI., "L'Astrologie dans le Monde Romain" and "Cumont," "Les Religions Orientales dans le Paganisme Romain" (Paris, 1907), Chap VII.

[63a] See Cumont, l'Influence religieuse de l'Astrologie dans le Monde Romain (Transactions of the 3d International Congress for the History of Religions, II., pp. 197–198).

[64] Bouché-Leclercq, pp. 624 seq.

[65] Compare for example the ideas associated with the planets in a modern manual of astrology like Ellen H. Bennett's "Astrology" (New York, 1897), pp. 93–100, with Bouché-Leclercq's statement of the Greek views ("L'Astrologie Grecque," pp. 93–101 and 311–326).

[66] Thibaut, "Astronomie, Astrologie und Mathematik," in Bühler-Kielhorn, "Grundriss der Indo-Arischen Philologie," III., 9, p. 15, and Kugler, "Kulturhistorische Bedeutung der babylonischen Astronomie," p. 49.

[67] It is one of the many merits of Bouché-Leclercq to have demonstrated

We thus find the source of all astrology in the ancient world in the system that arose in the Euphrates-Valley; and in view of this it will be admitted that the thorough study of Babylonian-Assyrian astrology is a factor of considerable importance in tracing the intellectual development of mankind. Coming back, therefore, to our immediate subject we have the curious phenomenon that about coincident with the period when a genuine science of astronomy takes a firm footing in Babylonia, astrology begins its triumphant march throughout the world. It is tempting to suppose that we have in this phenomenon the symptom of an "exchange" of influences that, while on the one hand Babylonia gave astrology to Greece, the contact with the scientific spirit of Greece resulted in giving an impetus to astronomical investigations in Babylonia. The possibility, indeed, of Greek influence on Babylonian astronomy was suggested by Bouché-Leclercq and is favored by Kugler.[68] Since, as now appears, the credit for the discovery of the precession of the equinoxes rests with the Greek astronomer, Hipparch, who announced it c. 130 B. C., and since it would indeed appear that in the second century B. C. the Babylonians, according to Kugler, were still ignorant of this principle, there is certainly every reason to suppose that the Babylonians were in this instance the pupils, and the Greeks the teachers. On the other hand, the Greek astronomers seem to have obtained from the Babylonians the names for the constellations of the ecliptic which we still use at the present time. Certainly, for the beginnings of their astronomy the Babylonians are not indebted to the Greeks since those beginnings reach back beyond the contact of Orient with

in his great work on Greek astrology the worthlessness of the traditions which ascribe Greek astronomy and astrology to an Egyptian origin. See especially the important note ("L'Astrologie Grecque," pp. 51–52) from which it appears that "Chaldean" and "Egyptian" are used almost interchangeably by uncritical Greek and Roman writers who hand down more or less fanciful traditions. Since Boll ("Sphæra," p. 159 seq.) and others have demonstrated the late origin of the zodiac of Denderah, the chief evidence for the early introduction of astronomy in Egypt has fallen away; and there is no reason for assuming that astrology flourished in Egypt before the Ptolemaic period.

[68] Bouché-Leclercq, *o. c.*, p. 50 and Kugler, "Kulturhistorische Bedeutung der babylonischen Astronomie," p. 48.

Occident, but that would not preclude the possibility of influences from the side of Greece at a later stage in the development of astronomical lore.

To account for the point of departure for the unfolding of a genuine science as astronomy, independent of merely empirical observations in the interest of astrology, and which as we saw[69] dates from the sixth century B. C., we have another factor entering into Babylonia about this time that must have exerted a profound influence—the appearance of Persia on the scene and with it the advanced form of faith known as Zoroastrianism and which by comparison with the emphatically polytheistic conceptions of the Babylonian religion was superlatively rationalistic. Contact with a strange culture is always attended by an intellectual stimulus, and this takes place whether the contest be friendly or hostile. Though the Persian rulers even after Darius with whom the full sway of Zoroastrianism may be said to begin, maintained a conciliatory attitude towards the gods of Babylonia, Cyrus going so far as to claim that his conquest of the country was in the interest of Marduk,[70] nevertheless, the presence of a totally different religion, recognized as the official one by the Persian rulers from the days of Darius on, must have acted as a disintegrating element that led to a decline in the belief in the Babylonian gods and to a corresponding weakening of the hold that the official rites had on the people. I venture to think that the influence of Zoroastrianism, bringing in its wake—as did Christianity and as did Islamism—a wave of intellectual advance, is the factor which accounts for the definite separation of the study of the heavenly phenomena from being merely an adjunct to a system of divination, to take its position as a genuine and independent science. A further impetus to the new science was given by the contact with Greek culture with the further possibility of a direct influence of Greek astronomical theories and methods on the investigations of the Babylonian priests.

The advance of astronomy must, however, have reacted also on the basic principle which we have seen underlay Babylonian-Assyrian astrology. Though even the *bârû*-priests, while still com-

[69] See above, p. 667.

[70] Hagen, Cyrus-Texte in "Beiträge zur Assyriologie," II., p. 229.

pletely enthralled by astrology, must have been impressed with the domain of law in the movements and phenomena of the heavens, there remained enough scope for caprice in the more unusual phenomena which the imperfect knowledge placed outside of the sphere of regularly working law. With the gradual reduction of this scope until through astronomical calculations even such phenomena as eclipses came within the range of recognized law, the belief in astrology must have suffered a decline, at all events in the minds of the better informed priests. Astronomy and astrology presented a contrast not unlike that which in modern times is frequently represented by science and religion and though no open conflict ensued, the growth of astronomy must have involved the decline of astrology. If the data of astrology are all due to the workings of inevitable and clearly recognized eternal laws, there is no room for any spontaneity on the part of the gods, so far at least as the stars manifest divine activity. Every advance in astronomy, therefore, removed a stone from the foundation on which the structure of astrology was reared, until the stability of the entire structure was endangered. The last three centuries before our era represent in general a period of declining faith in the gods both in Babylonia as well as in Greece and elsewhere. The old order throughout the ancient world of cultural development was passing away, and the growing strength of astronomy is in itself symptomatic of the new order destined to take the place of the old. It is no unusual phenomenon to find a great civilization handing over to posterity as a legacy at the period of its decay—a superstition instead of a real achievement. "The evil that men do lives after them; the good is oft interred with their bones" applies to nations as to individuals, and so it happens that while the wholesome fruits of the Babylonian-Assyrian civilization were not entirely lost, the overripe products with the odor of decay pervading them were the first to be exported to other climes. What became proverbial among Greeks and Romans as "Chaldaean wisdom" is not the astronomy of Babylonia but the astrology which, after having spent its force in the soil in which it arose, takes root elsewhere and soon flourishes more luxuriantly than it ever did in its native heath. We have, however, also seen that in the care of others the original plant was modified through the transfer from

the Orient to the Occident. Astrology in Babylonia declines as astronomy grows, for the very reason that astronomy is an outgrowth of astrology, representing the evolution of a science, by the breaking away from attachment to a religion and a cult. In Greece astronomy arises as do other sciences through the growth of the spirit of investigation. There was so far as we can see no religious tradition out of which or in opposition to which astronomy took its rise. There is no antecedent astrology from which astronomy emerges as the butterfly from the chrysalis. Therefore, astrology coming to the Greeks as a novel conception, with all the force of an apparently practical application of a scientific theory, suggesting the possibility of a direct communion with the arbiters of human fate—the conscious goal or unconscious hope of all religions—it was capable of being assimilated to the already firmly established astronomy. Astrology as further developed by the Greeks became merely one of the phases of astronomy, as is shown by the synonymity of the two terms, *ἀστρολογία* and *αστρονομία*[71]—a condition which persisted till mediaeval scholasticism, which distinguishes merely as a matter of definition between "natural astrology" or theoretical astronomy and "judicial astrology" or divination through the stars as the application of the theory to human life.

Lastly, if another suggestion be permitted, the "Chaldaeans" whom we encounter so frequently in Greek and Roman writers acting as "diviners" on such various occasions, appear to be indeed Babylonian *bârû*-priests or the disciples of these priests who, because of the decline of faith in astrology in the centers in which it arose, left their homes to seek their fortunes elsewhere. As with the growth of astronomical lore, the hold of the old system of astrology was loosened, the occupation of the *bârû*-priests was gone. Their condition was not unlike that of the Levites who, as the priests of the local sanctuaries in Palestine, were deprived of their standing and livelihood with the decline of these sanctuaries through the gradual concentration of Jahweh worship in the central sanctuary of Jerusalem. These Levites wandered to Jerusalem where, according to the Priestly Code, provision was made for them by assigning them to posts as assistants to the *kôhanim*—the legitimate priests of the cen-

[71] See Bouché-Leclercq, *o. c.*, p. 3, note 2.

tral sanctuary.[72] The *bârû*-priests of Babylonia in their capacity as astrologers wandered to the West, there to ply their trade for which a market was no longer forthcoming in their own homes. Babylonian astrology, enjoying the popularity in Greece and in the Roman empire frequently granted to a foreign importation in preference to a home industry, became the fashion of the Occident during the centuries that marked the decline of belief in the gods of Greece and Rome and that offered a hospitable welcome to all kinds of strange faith and mystic cults, until the term "Chaldaean" became synonymous with "astrologer." In time it was no doubt applied to the one who divined through the stars irrespective of his origin.[72a] Besides astrology, hepatoscopy was also practiced by these "Chaldaeans,"[73] but both forms of divination, being derived from an official cult and practiced purely as a profession that was presumably not without profit suffered, as was inevitable, a degeneration, with the result that a measure of reproach became attached to the term "Chaldaean," which acquired almost the force of trickster and deceiver. It was nevertheless fortunate that the term survived as a fingerpost, directing us to the land in which the system of divination arose that after strange vicissitudes has survived in the form as modified under Greek influences and with some additions in the mediaeval period, to our own days, still finding many devotees in circles where one would hardly expect to encounter them.[74]

The degenerating process through which the term "Chaldaean"

[72] See *e. g.*, Baudissin, Geschichte des Altestamentlichen Priesterhums (Leipzig, 1889), p. 287.

[72a] So, *e. g.*, Teukros, the author of a Greek treatise on astrology, is called "the Babylonian" evidently in the sense of "astrologer." See the fragments of this treatise published by Boll ("Sphæra," pp. 16–21) who places Teukros in the first century of this era.

[73] See the story told by Polyænus, "Strategicon," IV., 20, of the deception practised upon the army of Attalus I. of Pergamon by Soudinos "a Chaldæan augur" who writing the words "victory of the king" (*βασιλέως νίκη*) backwards on the palm of his hand, pressed the smooth side of the liver of a sacrificial animal on his hand, and then held the liver with the significant words inscribed on it to the gaze of the army, who regarded it as a sign sent by the gods. See also, above, p. 650, note 13.

[74] The late Richard Garnett is only one of many examples of men otherwise abreast with modern thought who cling to the faith in the revelations of the stars.

passed must not, however, lead us to the conclusion, which would be decidedly false, that astrology when it passed over to the West became wholly at the mercy of professional tricksters. This is but one phase of the subject which, seriously cultivated by Greek physicists, became bound up as we have seen with advanced forms of astronomy, mathematics and philosophical speculation. It is the old Babylonian astrology directly imported by "Chaldaeans" as professional astrologers that degenerated into a dishonest trade, whereas the modification of the Babylonian system under the influence of the Greek scientific spirit was raised to the dignity of a genuine science; and belief in it remained an integral part of science throughout the middle ages. In our days when the new scientific spirit has definitely broken with astrology, we are witnessing a process not unlike that which set in when faith in the Babylonian system declined in the land of its birth. Whatever justifiable basis (if any) it may have had is entirely obscured by those who exploit it as a profession. The modern "astrologers" are not the Greek astronomers attaching to their science a divinatory aspect, but the old *bârû*-priests in a new garb, plying a trade that flourishes through the readiness of people to be deceived—a readiness that amounts almost to willingness. Why then, it may be asked, search out the follies and superstitions of the past? Bouché-Leclercq[75] supplies us with the answer when he says "that it is not a waste of time to find out how other people wasted theirs."

[75] "L'Astrologie Grecque," p. ix.

FURTHER STUDIES ON TRANSPLANTATION OF VESSELS AND ORGANS.[1]

By ALEXIS CARREL.

(*Read, November 6, 1908.*)

It is known that tissues can be removed from an animal, transplanted into another animal and live normally in the body of their new owner. The transplantation of anatomical structures has already been, and will be again in the future, used in human surgery. For instance, an excellent method of treating an aneurism of the femoral artery would be the extirpation of the diseased part and its replacement by a piece of artery of same caliber. This new artery cannot be taken from an animal and grafted on man, for the serum of an animal is toxic for the cells of an animal of different species. A dog's vessel transplanted on man could possibly perform its arterial functions, but the histological structure of its wall would be deeply modified and accidents could occur. It is probable that arteries from anthropoid ape would be of safer use, because man and ape are closely related from a zoölogical standpoint. But this would be exceedingly expensive and not practical. It will be safer and simpler to graft on man vessels taken from another man. The vessels can be extirpated from an amputated limb or from the body of a criminal or of a man killed by accident. But it is sure that these cases will not present themselves at the time convenient for the surgeon and his patient. Therefore, it is important to find a method to store human vessels during the period which will elapse between their extirpation and their graft on the patient. With this view, I have attempted to preserve arteries in a condition of latent life, in order that, after having spent several days or several weeks outside of the body, they can be transplanted successfully.

[1] From the Laboratories of the Rockefeller Institute for Medical Research.

Before describing the method which renders possible the preservation of arteries, I shall briefly summarize some of the results obtained at the Rockefeller Institute in the transplantation of blood vessels and organs. These operations became possible as soon as a practical method of uniting blood vessels was found. Success in transplanting organs is direct function of the circulation. The circulation cannot be immediately reëstablished but by the sewing of the vessels of the organ to those of the host. The sewing of vessels is today a very easy operation. Some years ago, while I was working at the University of Lyons, I found a method of uniting severed arteries or veins, which gave excellent results. This method was progressively improved in such a manner that it is practically always successful. The vessels heal very quickly and no coagulation of the blood occurs when the operation is aseptic and the union of the vascular ends accurate. The scar of the severed vessels is, in many cases, so small that after a few months it is hardly discernible. On a renal vein examined a little over two months after the sewing, it was impossible to localize exactly the position of the anastomosis. The anastomosis of the renal artery was represented only by an indistinct line crossing the intima. Twelve months after the anastomosis of a carotid artery, the anatomical specimen was removed and examined. After longitudinal incision of the wall, no scar was seen on the intima, there was no modification of the caliber. But, in one small point, the vessel had lost part of its elasticity and it permitted to localize approximately the anastomosis. The results are permanent. Two and three years after the operation, the circulation through the anastomosis remains normal. It must be known also that, if the method is not correctly applied, or a fault of technique, even very slight, is made, thrombosis may occur. Success depends much less on the way of handling the needles or passing the threads than on the knowledge of the causes which are able to produce thrombosis and their removal. On human beings, this method has already been successfully used by American and European surgeons, and on animals, it has permitted to perform the transplantation of blood vessels, organs and limbs.

The graft of a segment of artery on an artery of another animal of the same species is ordinarily successful when the vessels are of

sufficient caliber. After a few months, the transplanted segment assumes exactly the same appearance as the normal vessel. The carotid of a dog was examined three months after the graft of an arterial segment. The transplanted segment was exactly similar to the other parts of the artery. There was no modification of caliber. The elasticity was normal. The only evidence of the operation was two whitish transverse lines on the intima. The remote results are excellent. A dog, into whose aorta a segment of aorta from another dog had been transplanted, was living and in good health nine months after the operation and the femoral pulse was normal. The transplantation of arteries has already been attempted in human surgery by Pierre Delbet in the treatment of aneurism. When a large artery is wounded and partially destroyed, or when a tumor adherent to the main vessels of a limb renders necessary the extirpation of these vessels, the substitution of a new piece of artery to the removed part would prevent the occurrence of gangrene.

The graft of an artery of an animal into an animal of different species is often successful if the animals are closely related. I transplanted several times segments of dog's carotid arteries on the abdominal aorta of cats with excellent functional results. Nevertheless, these results cannot be compared with those obtained in transplantation between animals of same species. Sometimes the lumen becomes dilated, or even a fusiform aneurism can be found. Even when the functions of the transplanted segment are perfect, its wall undergoes marked histological changes. The elastic framework disappears and progressively the muscular fibers are resorbed. After a few months, they have practically disappeared. The vessel is then composed mainly of connective tissue.

Veins can easily be grafted on arteries. I performed several times the transplantation of the vena cava on the aorta, on dogs and on cats, with excellent results. A segment of vein transplanted into an artery undergoes immediately very marked changes. The wall, which is very thin, becomes thicker and stronger. The lumen is often dilated, but no aneurism has ever been observed. On the contrary, the vein reacts against the increased blood pressure by thickening its wall. The thickening is due to an hyperplasy of the muscular cells and an hypertrophy of the adventitia. There is also

a very large increase of the interstitial connective tissue of the media. The venous wall becomes as strong as the arterial wall. The function has created the organ. Therefore, veins can act as a substitute for arteries. This is of practical importance in human surgery, for on the patient himself an abundant supply of vein can always be found.

The organs, kidneys, spleen, or thyroid gland, for instance, can be transplanted from an animal to another animal and their circulation immediately reëstablished by suture of the blood vessels to those of their host. Two methods are used—the simple transplantation, and the transplantation in mass. The simple transplantation consists of dissecting the organ, cutting its vessels, and uniting these vessels directly to those of the host. In the transplantation in mass, the organ is extirpated, together with the surrounding tissues and organs, its nerves, vessels and the main vessels of the region. After transplantation, the anastomoses are not made on the vessels of the organ themselves, but on the main vessels of the anatomical region. The transplantation in mass of the kidneys has been performed on cats. It consists of extirpating from a first animal both kidneys, their vessels and the corresponding segments of the aorta and vena cava, their nerves and nervous ganglia, their ureters and the corresponding part of the bladder; of placing these anatomic specimens into the abdominal cavity of a second animal whose kidneys have been previously resected and the aorta and vena cava cut transversely; and of suturing the vascular segments between the ends of the aorta and vena cava, and of grafting the flap of bladder onto the bladder of the host. In every case the reëstablishment of the renal functions was observed. These functions were determined by the character of the urine and the general condition of the animals.

The secretion of urine often begins as soon as the arterial circulation is reëstablished. In some cases the amount of urine during the first twenty-four hours was more than 100 c.c. However, a cat urinated only 25 c.c. during the first twenty-four hours; the second day the amount of urine passed was only 16 c.c.; this urine was highly concentrated and contained much urea. Every cat urinated abundantly every day, but the animals presented sooner or later

some complication, which modified in some measure the renal functions. As is to be expected after an operation as complex as the transplantation in mass, various accidents occurred; hydronephrosis, intestinal compression by peritoneal adhesions, volvulus, phlegmon, puerperal infection, compression of the renal veins by organized hematoma of the connective tissue, which were the direct or indirect causes of death in these animals. However, in two experiments the functions of the kidneys seem to have been for a certain time almost completely normal. The color of the urine was yellow, generally, or often less dark than the normal urine of the cat. Its reaction was acid. Its quantity for twenty-four hours oscillated between 120 and 160 c.c., but it might be, exceptionally, 25 and even 15 c.c., or in another case, 215 or 255 c.c. for twenty-four hours. The density was very far from constant; generally it oscillated between 1.018 and 1.030, going sometimes as high as 1.035 and 1.051. Among the abnormal constituents of the urine the presence of albumin only has been looked for. In some cases there was a little albumin during the first days, ranging from 0.50 to 0.25 for 1,000 c.c. In other cases the albumin disappeared about one week after the operation.

The general condition of the animal can be used, in some measure, to indicate the perfection of the urinary elimination. As long as no complications were present the animals lived as normal cats do, without presenting any symptoms which could be considered as produced by renal insufficiency. When general complications occurred the cats reacted against them in normal ways. In one case, the animal was in apparently normal condition four days after the operation. She walked about the room, played and ate a great deal of raw meat. Her condition remained excellent for several weeks. Twenty days after the operation she was in good health, had glossy hair, was very fat, ate with appetite all kinds of food and urinated normally. There was, however, albumin in the urine, and slow and progressive enlargement of the kidneys took place, which showed that she was not in an entirely normal condition. It remained in excellent health until the twenty-ninth day after the operation. Then gastro-intestinal symptoms appeared, and death occurred on the thirty-first day after the operation.

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In another experiment the animal was a female cat which had lived in the laboratory for several months. She was in excellent condition when she was operated on and recovered very quickly from the operation. Her life went on just the same as before. The kidneys were movable and small. She looked in excellent health and lived as a normal cat. On the eighteenth day after the transplantation albumin appeared in the urine and a direct examination of the kidneys was made to ascertain the cause. The general condition was little affected by the operation and the albumin disappeared on the twenty-first day, but reappeared again a little later. On the thirty-fifth day the animal was very weak and emaciated. She died on the thirty-sixth day of acute calcification of the arteries.

These results show that the functions of the kidneys reëstablished themselves after the transplantation. Since an animal can live in an apparently prosperous condition of health fifteen or twenty-five days and more, after a double nephrectomy, and eliminate each twenty-four hours from 120 to 160 c.c. of urine through the new kidneys, it is certain that the functions of the transplanted organs are efficient.

The " simple transplantation " of the kidneys consists of dissecting a kidney, cutting the renal vessels and ureter a few centimeters below the hilus, implanting the organ on the same or another animal, and of anastomosing its vessels to the renal vessels of the host. I performed the double nephrectomy and the replantation of one kidney in five dogs. The secretion of the urine remained normal as long as no ureteral complication occurred. The conditions of the kidneys were excellent. A little more than two months after the operation, the location of the anastomoses of the renal vein could not be detected. The anastomosis of the renal artery was seen as a small and indistinct line on the intima.

The remote results of this operation are excellent. On February 6, 1908, the left kidney of a middle-sized bitch was extirpated, perfused with Locke's solution and put into a jar of Locke's solution at the temperature of the laboratory. The ends of the vessel were prepared for anastomoses, and afterward the kidney was replaced into the abdominal cavity. The circulation was reëstablished after suture of the vessels and the ends of the ureter united. The animal

made an uneventful recovery. Fifteen days afterward the right kidney was extirpated. The animal remained in perfect health. The urine did not contain any albumin. It is generally of low density. Today the animal is in perfect condition. (Fig. 1.)

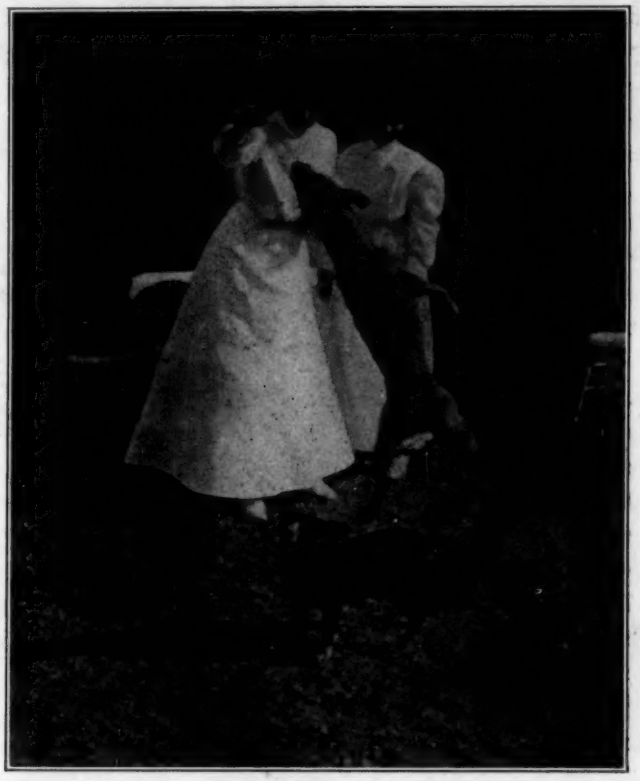

FIG. 1. The dog, who is jumping, underwent nine months ago a double nephrectomy and replantation of one kidney.

This observation demonstrated definitely that an animal can live in normal condition after both kidneys have been extirpated and one replaced. It removes also, without need of further discussion, the objections of the experimenters who claim that the section of the renal nerves, the temporary suppression of the renal circulation or the perfusion of the kidneys produce necessarily dangerous and even fatal lesions of this organ.

By using the method of transplantation in mass it becomes possible to perform the transplantation of a whole anatomic region, with its main artery and vein. From a first dog, the right part of the scalp and the auricle were extirpated in one mass wtih the cartilaginous portion of the auditory canal cut close to the skull, the connective tissue and the glands of the retro-maxillaris space, the tissues of the carotid region, and the upper portions of the external jugular vein and of the common carotid artery. On a second dog the auricle and a portion of the scalp was extirpated and the right part of the neck opened through a longitudinal incision. The anatomic specimen was then placed close to the wound, and the peripheral end of the carotid artery and of the jugular vein united to the central end of the corresponding vessels of the host, at the level of the middle part of the neck. The circulation was then reëstablished. Then the neck was closed by two rows of suture. A few minutes after the establishment of the circulation the ear and the scalp assumed their normal appearance. The new ear was fixed by circular suture of its cartilaginous canal to the cartilaginous canal of the host. The auricular muscles were sutured and the operation completed by continuous catgut suture of the skin without drainage.

Three weeks after the operation the auricle and the transplanted tissues were in normal condition. The temperature of both auricles, normal and transplanted, were about the same. The transplanted ear was as thin and glossy as the normal one. Except for the difference of color, it could not have been seen that the ear did not belong to the dog.

The transplantation of a limb from one animal to another of the same species is a problem very much simpler than the transplantation of a gland. In April, 1907, I found that a thigh, extirpated from the fresh cadaver of a dog, and transplanted onto another dog, could begin to heal in a very satisfactory manner. One year after, by using more careful asepsis in the transplantation of the leg from one fox terrier to another, I observed union by first intention of the new leg to its host.

A white, middle-aged male fox terrier was etherized and the left leg cut just below the knee. The limb was perfused with Locke's solution, wrapped in a greased silk towel and kept on a table at the

temperature of the laboratory. A white, young female fox terrier was etherized. She was of the same size and shape as the first dog. Her nails and bones were very slightly smaller. The leg was amputated circularly just below the knee. The new leg was immediately fixed to the central end of the tibia of the host by an Elsberg's aluminum splint. The muscles, nerves and femoral vessels were united to the corresponding parts of the host, and the circulation reëstablished. A small exploratory incision was made between the second and third toes. Hemorrhage of red blood occurred. The animal recovered quickly and remained in normal condition. The temperature of the new foot was at first higher than that of the normal one. It was also edematous. After a few days the edema disappeared and the foot had exactly the same appearance as the normal one. The temperature went slightly down. There was only a difference of one tenth of a degree centigrade between the normal and the new foot.

Fifteen days after the operation the new leg was perfectly healed by first intention, but the bones were not very strongly united. The Elsberg splint had broken and the tibia was a little incurved. The exploratory incision of the foot, although having been slightly infected, was completely cicatrized. The new leg had the same appearance as the normal one. The animal was in good condition, but coughed a little. At this time several other dogs died of broncho-pneumonia. The animal became sick. Twenty days after the operation her condition became worse and a marked dyspnea appeared. The dog died on the twenty-second day after the operation. Postmortem examination showed a double diffuse bronchopneumonia. The new leg was perfectly healed; with linear cutaneous scars. Its appearance was exactly the same as the normal leg. The bones were strongly united by a fibrous callus. The exploratory incision of the foot had healed without visible scar.

This experiment is the first example of successful grafting of a new limb on an animal. It demonstrates that the leg, in spite of the change of owner, remains normal. If further experiments show that the functions of the transplanted limb are normally reëstablished, it will be permissible to try on man the transplantation of

limbs, or segments of limbs, taken from an amputated limb, or from the body of a man killed by accident.

All these experiments show that the remote results of the transplantation of fresh vessels can be perfect, that transplanted kidneys functionate, that an animal having undergone a double nephrectomy and the transplantation of both kidneys from another animal can live normally for a few weeks, and that an animal which has undergone a double nephrectomy and the graft of one of his own kidneys can recover completely and live in perfect health. Finally, it has been demonstrated that a leg extirpated from a dog and substituted for the corresponding leg of another dog heals normally.

Since the experimental transplantation of arteries are permanently successful, it is permissible to use this method in human surgery; for instance, in treating aneurisms as it has been already tried by Delbet in Paris. The era of these operations being opened, the attempt of preserving blood vessels outside of the body in a condition of latent life was made with the view of rendering these operations more practicable.

The length of the period which elapses between the extirpation of a tissue, and the reëstablishment of its circulation after transplantation, is an important factor of success or failure. The result of the graft depends entirely on the condition of the tissues at the time of the reëstablishment of the circulation. They must still be alive; although apparently dead. If the tissues are really dead, the graft is completely unsuccessful. There are two kinds of death, general death or death of the whole organism, and elemental death or death of the tissues and organs. It is impossible to give a definition of general death. Everybody understands what it means. Nevertheless, we are as ignorant about it as about life. General death can occur suddenly, while elemental death is a slow process. A man, for instance, is stabbed through the heart and killed. His personality has disappeared. He is dead. However, all the organs and tissues, which compose the body, are still living. The life of every tissue and organ of the body could go on if a proper circulation was given back to them. If it were possible to transplant immediately after death the tissues and organs, which compose this body, into other human organisms, no elemental death would occur, and

all the constituent parts of the body would continue to live. The man, however, would be dead, for his personality would have disappeared. In this case, general death can be defined as the rupture of the contract of association between the tissues and organs of the organism by failure of one of the partners, the heart. Therefore, general death is very different from elemental death. It is merely the starting point of the disintegrative phenomena which lead to elemental death.

Immediately after general death, elemental death begins. It is a complex and slow process which progressively destroys the living matter. We cannot know directly whether or not a tissue is living and by what chemical or physical peculiarities a living being differs from its corpse. There is no reagent of life. Living matter, in a condition of non-manifested life, is apparently similar to non-living matter. We perceive life only through its manifestations. Our ignorance renders for us unmanifested life similar to death. If seeds or microbes are placed in physico-chemical conditions, where manifested life is impossible, living matter canot be distinguished from dead matter. What is the difference between a dead seed and the seed which will produce a large tree? We do not know. Between a vessel which will live normally after transplantation, and another one which will undergo deep microscopical lesions, there is no morphological difference. We know merely that, immediately after general death, the tissues are still alive, because they manifest life if they are given back their normal circulation. We know also that some time after general death they die, because they are not able to manifest life again, even when replaced in normal physiological condition. Between the death of the organism and the elemental death there is a period where the tissues are progressively invaded by cadaveric disintegration. At the beginning, the cadaveric changes are slight, and the tissues can recover if placed back into normal condition. Later, irreversible changes take place and elemental death, that is, destruction of the living matter, occurs.

The duration of this period intermediate between death of the organism and elemental death is longer or shorter, according to the nature of the tissue. The cerebral substance disintegrates so quickly that, after a few minutes of complete anemia, irreparable lesions

take place. The spleen, liver and kidneys are also rapidly destroyed. On the contrary, the anatomical structures which compose a limb are very strong and can overcome for a long time the cadaveric processes. The different parts of the same organ do not present similar resistancy to cadaveric disintegration. Among the anatomical components of renal substance, the cells of the secretory tubules are extremely delicate and may present marked morphological changes a short time after death. The cells of the excretory tubuli are stronger. The glomeruli are still more resistant. It may happen that the epithelial cells are already dead, while the glomeruli and the vessels are still living. The vascular endothelium seems to be the "ultimum moriens" of the organ, according to Wells. The vessels, which are the necessary condition of life of organs, are also the part of the organs which resists longer the disintegrative processes. The elements which compose the wall of an artery differ widely in resistancy. The muscular fibers die first. Immediately after the stopping of the circulation, all the elements of the vascular wall are alive. If the transplantation is performed at this moment, the artery lives in the body of its host and keeps its normal constitution. If the transplantation is performed a little later, when the muscular fibers are already dead, the wall of the artery will be composed mainly of connective and elastic tissue, and the muscular fibers will disappear. If the artery is completely dead when the transplantation is made, its wall will be composed of amorphous substance, around which the organism will create an envelope of dense connective tissue.

Elemental death is brought about by microbian and autolytic enzymes. Immediately after general death, the microörganisms from the digestive tract diffuse through the body and their ferments begin to destroy the tissues. At the same time, the autolytic ferments, which are not any longer held in check by the serum, contribute also to the disintegration of the organs. This destructive process is increased or retarded by the causes which activate or retard the enzymotic actions, and the multiplication of the microorganisms. For instance, the rate of cadaveric disintegration, which is very rapid at 35° or 40° C., becomes very slow at + 1° or + 2° C. It is completely stopped by desiccation of the tissues. The preser-

vation of the tissues in the serum of the same animal will also retard very much the organic destruction.

The occurrence of cadaveric changes in tissues, which will be used for transplantation, must be prevented. This can be attained in two different manners: by stopping completely the chemical activities of the tissue, or merely by retarding so much the evolution of autolytic disintegration that, after a few days or a few weeks, the lesions are so small that they are not dangerous.

The first method would be ideal. The tissue, being in a condition of chemical indifference, could be preserved theoretically for an indefinite period. There are many instances of this form of latent life in the animal kingdom. Two centuries ago, Loevenhoeck obtained the resurrection of *Milnesium tardigradum,* which had been completely dried for a long time, by moistening it with water. In 1840, Doyere studied also the peculiarities of latent life of *Milnesium tardigradum.* He dried completely a few of these animals, heated them at a temperature of 100° C., and, after having humidified them, observed that they lived again. These observations are very important because *Milnesium tardigradum* is highly organized and contains muscular fibers, nerves, nervous ganglia, etc. Paul Bert, in several famous experiments, attempted to preserve tissues of mammals in a condition of latent life. One of those experiments consisted of cutting the tail of a rat, drying it in vaccum, and submitting it to a temperature of + 100° C. The tail was afterwards transplanted onto another rat. It was observed that the dimensions of the tail grew larger, that its vessels united to the vessels of the host and that the bone marrow underwent fibrous degeneration. It showed that the heated and dried tail could live again. I attempted to preserve arteries in latent life by a similar method. Carotid arteries from dogs were extirpated and placed in sealed glass tubes, part of which were filled with calcium chloride. Within a few hours, the arteries became yellow brown, shrank and looked like pieces of catgut. One tube was heated for twelve minutes at + 100°. When, after several days, the dried vessels were put into Locke's solution, they took back their water and assumed again their normal color, size and consistency. Two of them were transplanted onto the carotid arteries of dogs. It was found that they could

perform normally their functions. Two weeks after the operation, one of the vessels was examined. The circulation was normal. The transplanted segment looked very much like the other parts of the carotid. It was covered by a normal connective tissue sheath. The wall was of same color and thickness as the wall of the normal carotid. Its consistency was a little harder. Nevertheless, it was found, by microscopical examination, that this wall was composed of an elastic framework and amorphous material surrounded by a new wall of connective tissue. The vessel was dead. The death of the vessel was perhaps due more to the way in which the desiccation was done than to the desiccation itself. With a better technique, results similar to those of Paul Bert could possibly be obtained. Actually, this method is dangerous because the artery is not any longer a living structure, but merely a foreign body, as a piece of rubber tubing or an artery preserved in formalin or killed by heating.

The second method of preserving arteries, outside of the body, consists in lowering the power of the microbian and autolytic enzymes, by keeping the tissues at a low temperature. This method cannot suspend, for an indefinite time, the occurrence of elemental death. It increases only the length of the period during which the cadaveric changes are slight and not able to interfere with a complete, or almost complete, recovery of the artery after transplantation. If a vessel is extirpated aseptically, placed in a sterilized sealed tube and kept in a refrigerator just above the freezing point, it can be preserved for a long time in good condition. From a surgical standpoint, it is sufficient that the vessels are kept safely for a few days outside of the body before being transplanted. Nevertheless, it is far from perfect. The ideal method would be certainly to place the tissues in a condition of latent life, as is possible for *Milnesium tardigradum* and other organisms.

The technique that I use is very far from being original. The vessels are merely preserved in cold storage as are commonly eggs, or chickens, or vegetables. They are removed from a living or a dead animal soon after death, perfused and washed with Locke's solution and placed in sterilized glass tubes, the atmosphere of which is moistened with a few drops of water. The tubes are immediately

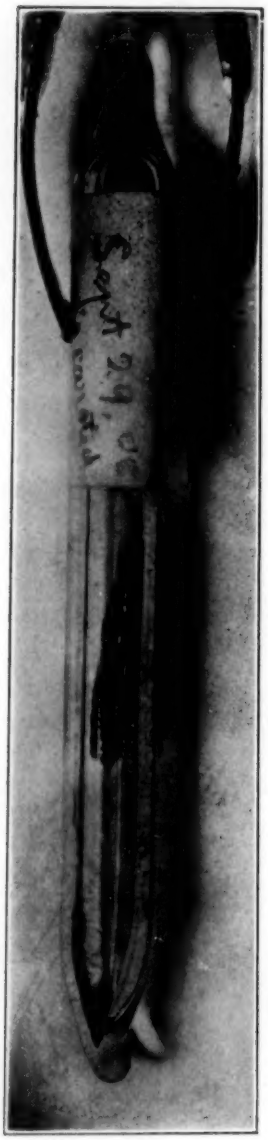

FIG. 1.

FIG. 2.

FIG. 1. Segment of artery preserved in a sealed sterilized tube.

FIG. 2. Segment of artery preserved for twenty two days in cold storage. Six months after transplantation.

sealed. (Plate VII, Fig. 1.) Sometimes, the arteries are put in a fluid. A few vessels have been preserved in isotonic sodium chloride solution. The result was unsatisfactory; for the muscular fibers of the artery were killed in twenty-four hours. The results obtained with Locke's solution were much better. However, a still better method would consist in keeping the vessels in serum of an animal of the same species or in inactivated serum of an animal of different species. The serum is more exactly isotonic for the tissues than Locke's solution; it is slightly bactericidal, and it contains antibodies for the autolytic ferments of the cells. I performed once only the transplantation of a segment of dog's carotid, preserved in dog's serum for forty-eight hours. Fifteen days after the transplantation, the vessel was examined and found in a perfect microscopical condition.

The sealed tubes containing the arterial segments are put into a thick-walled ice-box, the temperature of which remains constantly between 0 and + 1° C. The temperature must not go down below 0° C. When the vessels have been frozen, the wall presents soon after the transplantation marked microscopical lesions. If the temperature is too high, and the operation not thoroughly aseptic, microbian colonies may settle in the wall of the vessels. Obliteration or development of fusiform aneurism are the consequence of these faults of technique. When the operation has been correctly performed, the artery keeps its normal appearance for a long time. After several weeks, its color and consistency are generally normal. The wall is a little softer and the vessel flattens itself more easily. After six, seven and even ten months, the macroscopical appearance of the vessel is not markedly modified. Sometimes it looks completely normal. From a microscopical standpoint, the condition of the arteries is very variable. In some cases, the nuclei of the muscular fibers are modified. In other cases they are absolutely normal. A section of a pig's carotid artery, preserved in a sealed tube with a few drops of Locke's solution from April to November, 1908, was entirely normal. It looked as if it had been extirpated from the animal a few moments before being fixed in Zenker's fluid, while it had been preserved for six months outside of the body.

A few minutes before the transplantation, the tube is removed

from the ice-box and broken. The vessel is removed from the tube, put in a jar of Locke's solution at the temperature of the laboratory, thoroughly washed and placed in warm vaseline. Afterward, the vaseline is expressed from its lumen, and the segment grafted onto the artery of the host. As soon as the circulation is established through the artery of the host, the transplanted segment, which is white, takes back immediately its normal color and becomes almost similar to the other parts of the artery. Sometimes the small vessels of the adventitia appear neatly injected with blood. In segments of carotid artery, preserved for eight and eleven months in cold storage and grafted on the carotid of a dog, the vasa vasorum were seen full of blood as soon as the circulation was reëstablished.

The results of the transplantation of arteries, preserved in cold storage, are generally excellent from a functional standpoint, even if the vessel has been kept for one or two months outside of the body. But, from an anatomical standpoint, the microscopical constitution of the vessel is markedly modified when it has spent a long time in cold storage. The duration of the period during which a vessel can be preserved without occurrence of any lesion, is not exactly determined. However, it seems that an artery, preserved for more than eight days in cold storage, undergoes always, after transplantation, a degeneration of its muscular fibers, while the other parts of the vessel seem to remain normal. Several times a perfect histological condition of the transplanted artery was observed. A piece of carotid artery from a dog was put in a sealed tube with a few drops of Locke's solution and, two days afterward, transplanted onto the carotid artery of another dog. Two weeks after the operation, the neck of the dog was reopened. The circulation through the carotid was normal. The transplanted segment looked like the other parts of the carotid. It was resected and examined histologically. The adventitia was thickened and contained several small vessels. The media was normal. The nuclei of the muscular fibers were found entirely similar to those of a normal artery. The intima was well preserved and slightly thickened. This observation shows, evidently, that a vessel can be preserevd in cold storage and live again normally when transplanted. It is not a dead, but a living artery, with all its normal anatomical elements.

Thus, the vessel, while in cold storage, was in a condition of unmanifested life.

The behavior of a vessel, transplanted after having been killed, by formalin or by heating at 80° C., is different. Often its appearance is normal, from a gross anatomical standpoint. Nevertheless, a few days after transplantation, its microscopical constitution is deeply modified. Its wall is composed of an amorphous material where no nuclei can be observed, but where the elastic framework still is visible, although very modified in its shape. The wall is surrounded by a layer of connective tissue produced doubtless by the host. A dead vessel is merely a foreign body, which would progressively be resorbed and replaced by connective tissue. Thrombosis frequently occurs after this kind of transplantation and its use is dangerous from a clinical standpoint. On the contrary, a vessel, preserved for a few days in a condition of latent life, is still a living structure when it is transplanted. Its use is as safe as that of a fresh artery.

In all the cases where the vessels spent more than eight days in the ice-box, the muscular fibers of the media disappeared a few days after transplantation. Nevertheless, the anatomical results were often so perfect that, after a few months, the location of the transplanted segment on the artery of the host was hardly discernible. On April 2, 1908, a piece of carotid, preserved for twenty-two days in cold storage, was transplanted on the carotid of a dog. On October 15, 1908, the neck was opened and the carotid dissected. It was not possible to find the location of the transplanted segment. After longitudinal opening of the carotids, the location of the anastomoses could be determined. (Plate VII, Fig. 2.) The result of the graft of a vessel which had spent seventy days in cold storage was as satisfactory. Six months after the operation a section was made through the middle part of the transplanted segment. The adventitia was normal and the intima thickened. The media was composed of elastic fibers which had retained their ordinary wavy appearance. All the muscular fibers had been destroyed.

The actual method failed to give positive results in the transplantation of arteries after several months in cold storage. Graft of arteries which had spent eight months outside of the body was

attempted in two cases. Thrombosis occurred. The vessels were dead, and, in spite of their almost normal appearance, markedly disintegrated.

The remote results of the transplantations of preserved vessels are very satisfactory from a clinical standpoint. In November,

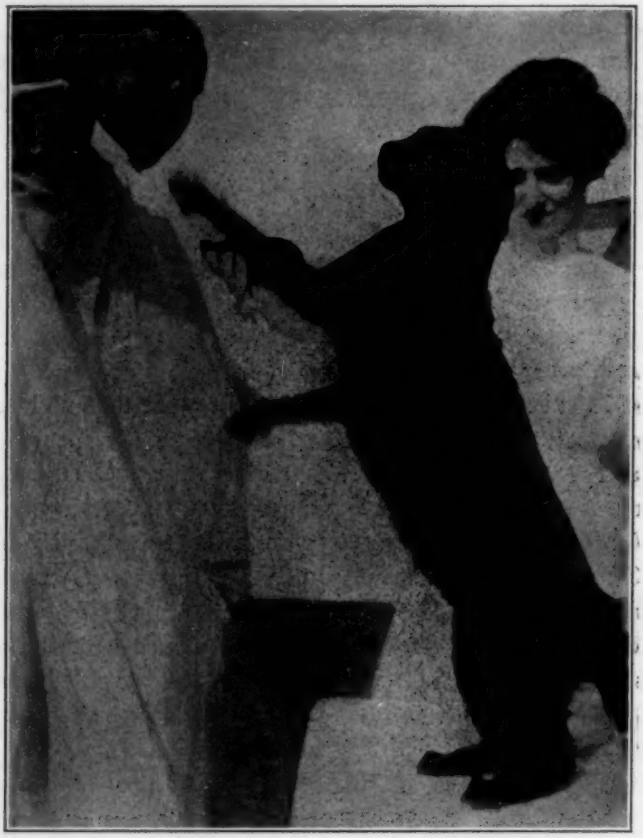

FIG. 2. Cat in which a segment of the abdominal aorta was replaced by a piece of dog's carotid.

1906, a segment of the abdominal aorta of a cat was extirpated and replaced by a piece of dog's carotid preserved in cold storage for twenty days. The animal remained in excellent health. After a few weeks, the abdomen was reopened and the transplanted artery

examined. The circulation through the new artery was excellent, and its caliber normal. The abdomen was closed. The cat spent the years 1907 and 1908 at the Rockefeller Institute in excellent health. The femoral pulse was normal. The condition of the femoral pulse is an indication of the condition of the circulation through the abdominal aorta. Partial or complete occlusion of the aorta produces diminution or disappearance of the pulse of the femoral arteries. To-day, twenty-five months have elapsed since the operation, the cat is in good condition (Fig. 2) and the femoral pulse normal.[2]

FIG. 3. Dog in which a segment of the abdominal aorta was replaced by a piece of human popliteal artery.

In May, 1907, a short portion of the abdominal aorta of a small bitch was extirpated. Between its cut ends was grafted a segment of popliteal artery from a young man's leg amputated at the Presbyterian Hospital by Dr. Ellsworth Eliot. Before being transplanted, the popliteal artery had been preserved for twenty-four

[2] This cat was presented before the American Physiological Society, December 1906.

days in cold storage. The femoral pulse remained normal. A few months after the operation, the abdomen was reopened and the circulation through the new artery found normal. There was no modification of its caliber. The animal remained in good health. During the years 1907 and 1908, no modification of the femoral pulse occurred. It is still normal to-day, one year and a half after the operation, and the animal is in excellent condition (Fig. 3).

These experiments demonstrate that the clinical results of the transplantation of preserved vessels can remain satisfactory for a long time. However, in both cases, the operation was performed under unfavorable circumstances. The grafted arteries belonged to an animal of different species and the method of preservation used in both cases was imperfect. The wall of these vessels underwent certainly marked histological changes. Nevertheless they are still able to perform normally their functions.

Conclusions.

The results of the experiments of preservation of arteries in cold storage must be considered from both the anatomical and the practical standpoint.

From an anatomical standpoint, they show that an artery from an animal can be kept outside of the body for two days at least, transplanted onto another animal of the same species, and live again without presenting any change of its constituent elements. The transplantation of vessels killed by drying, heating or fixation in formalin is followed by degeneration of the wall and replacement by connective tissue from the host. When the vessel is kept in cold storage for a longer period of time, all the muscular fibers of the media disappear a few days after transplantation. If the period spent in cold storage is still longer, eight months for instance, thrombosis occurs.

From a practical standpoint, these experiments demonstrate that the preserved vessels, even if their muscular fibers are completely resorbed, are an excellent substitute for arteries and perform normally their functions for months and years.

Stated Meeting November 20, 1908.

President KEEN in the Chair.

The decease was announced of Prof. William Keith Brooks, at Baltimore, on November 12, 1908, æt. 60.

The following papers were read:

"The Early History of the American Philosophical Society," by Mr. Joseph G. Rosengarten.

"The Recapitulation Theory of Embryologists," by Prof. Thomas H. Montgomery, Jr., which was discussed by President Keen, Prof. Kraemer, Prof. Doolittle, Prof. Pratt and Prof. Montgomery.

Stated Meeting December 4, 1908.

President KEEN in the Chair.

Prof. Edwin G. Conklin read an obituary notice of Prof. William Keith Brooks (see page iii).

The following papers were read:

"Astrology in Ancient Babylonia," by Prof. Morris Jastrow, Jr. (see page 646), which was discussed by President Keen and Mr. Goodwin.

"On the Effect of a Radio-Active Mineral on Plant Growth," by Mr. Joseph Willcox.

Dr. John L. Shober exhibited some photographs made by radiations from radium and uraninite.

Stated Meeting December 18, 1908.

PRESIDENT KEEN IN THE CHAIR.

Professor Herbert Weir Smyth, a newly-elected member, was presented to the chair and took his seat in the Society.

A letter was read from the Geological Society of Glasgow stating that it would celebrate its jubilee on January 28, 1909, and inviting the Society to be represented thereat. The invitation was accepted and Sir William Turner, K.C.B., was appointed the Society's representative.

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The decease was announced of

Dr. Ernest T. Hamy, at Paris, on November 18, 1908, æt. 65.

Prof. Oliver Wolcott Gibbs, at Newport, R. I., on December 9, 1908, æt. 86.

Professor Herbert Weir Smyth read a paper on "Ancient Greek Conceptions of the Future Life" which was discussed by Professor Lamberton, Professor Newbold and Professor Smyth.

Special Meeting December 21, 1908.

PRESIDENT KEEN IN THE CHAIR.

The President introduced Professor Guglielmo Ferrero, who read a paper on "Antony and Cleopatra."

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OBITUARY NOTICES

OF

MEMBERS DECEASED

William Keith Brooks.

William Keith Brooks was born at Cleveland, O., March 25, 1848, and died at his home, "Brightside," near Baltimore, November 12, 1908. His parents were born in Vermont, but their ancestors had lived for many generations at or near Concord, Mass., the first of the name having come to America from England prior to 1634. Young Brooks received his early education in the public schools of Cleveland, and he afterward entered Hobart College, Geneva, N. Y., where, he says, "I learned to study, and, I hope, to profit by but not to blindly follow, the writings of that great thinker on the principles of science, George Berkeley." He spent two years at Hobart, where he took high honors, and then entered the junior class at Williams College. Here he distinguished himself as a thorough and independent scholar, and is said to have been one of the most brilliant students in mathematics Williams had ever known. In 1870 he received the degree of bachelor of arts and was elected to Phi Beta Kappa.

After his graduation his father took him into mercantile business with himself, intending that he should become his successor, but such work was distasteful to young Brooks and he soon abandoned it and became a teacher in a boys school at Niagara, N. Y. When he left college he was undecided whether to devote himself to mathematics, to Greek, or to biology, for he was unusually proficient in all of these subjects. He was an enthusiastic naturalist; even as a boy he had given much attention to fresh-water aquaria and to the habits of animals, and he had published some of his observations; with one of his friends he had constructed a microscope and with other associates he had organized a class in natural history; he had also read many books on natural history and was intensely interested in evolution and Darwinism. He finally decided to devote himself to biology, largely influenced, we may imagine, by the philosophical importance of this subject.

At Harvard Louis Agassiz was at the climax of his wonderful career, and thither flocked many young men, who afterward became leaders in biological science, to study under this great master; among these was Brooks. In the summer of 1873 he was a student at Agassiz's laboratory at Penikese, and from that time until his death he remained a student of marine life. The sea with its teeming multitudes of living things always had a particular charm for him, not merely because of the interest and variety of its forms of life, but also because it was the scene of the earliest acts in the drama of evolution.

In 1875 he received the degree of Ph.D. from Harvard University and was appointed assistant in the museum of the Boston Society of Natural History. On the founding of the Johns Hopkins University in 1876 Brooks applied for and obtained one of their twenty famous fellowships, which have done so much to change the character of university work and ideals in this country. Before he entered upon his fellowship his abilities as a teacher were recognized and he was appointed associate in biology. In 1883 he was appointed associate professor of morphology and in 1889 professor in that subject. On the retirement of Professor H. Newell Martin from the headship of the Biological Department in 1894, Professor Brooks became head of the department and continued in that position until his death. His active scientific life was therefore coextensive with that of the Johns Hopkins University, and his love of the Biological Department and his loyalty to his University were among his strong characteristics.

Although his publications were numerous and important I think that his influence was greatest and most far reaching in his work as a teacher and scientific director. To few biologists, perhaps to no other in the history of this country, has it been given to direct the work and shape the scientific ideals of so large and influential a body of young men. Among those who took their doctor's degrees under him are more than a score of the leading zoölogists of this country, while many other distinguished scholars of this and foreign lands were his pupils.

Although Professor Brooks would present a subject in his lectures in a most clear and entertaining manner, he rarely if ever

attempted to smooth the path of the investigator; the latter was to a very large extent thrown upon his own resources. He believed so thoroughly in the law of natural selection, as he once told me, that he thought it was best for a student to find out for himself, as soon as possible, whether he was fitted for independent investigation or not, and by this rigid discipline the unfit were weeded out from the fit. This was certainly no school for weaklings, but it afforded magnificent training for those who had ability and determination. For those who endured this ordeal he maintained the warmest regard, and his interest and pride in the work of his students was as marked as it was stimulating.

In connection with his work as teacher and director must be mentioned the establishment by him of the Chesapeake Zoological Laboratory in 1878. This was the second marine laboratory in this country founded for advanced work in pure zoölogy. The first was established by Louis Agassiz on the island of Penikese in Buzzards Bay in 1871. The Chesapeake Laboratory, unlike the one at Penikese, was not limited to one place, it consisted neither of buildings nor equipment, but of men and ideas. For the first few years of its existence it was located at several different points in Chesapeake Bay; afterwards it was located at Beaufort, N. C., then at different places in the Bahama Islands, and finally in Jamaica. In the various expeditions of Brooks and his students to these different places they made not only a thorough biological survey of each region, but they did work of most fundamental and far reaching importance on the various groups of animals found. Out of these expeditions has grown the beautiful and permanent station of the U. S. Fisheries Bureau at Beaufort, N. C., in which Brooks took great interest and pride.

The "Scientific Results of the Sessions of the Chesapeake Zoölogical Laboratory" were at first published as a separate journal of which Brooks was the founder and editor, later this was incorporated in the "Studies from the Biological Laboratory" of which he was joint editor with H. Newell Martin. He subsequently established and edited "Memoirs from the Biological Laboratory," a large quarto for the publication of important monographs. He

was also one of the editors of the "Journal of Experimental Zoölogy."

As a scientific investigator Brooks showed sound judgment, depth of insight, and untiring industry and enthusiasm. In his research he did not attempt to cover the whole field of zoölogy, but he did attempt to do thoroughly and well all that he undertook. His work began at a time when descriptive embryology was the newest and most promising branch of zoology and much of his earlier work was devoted to this field. His first important paper was on the "Development of *Salpa*," and many of his later works, some of them monumental monographs, were devoted to the anatomy, embryology and evolution of this interesting group of ascidians. Indeed his latest work which was left in manuscript and for which he had prepared hundreds of beautiful drawings, was a continuation of his great "Monograph on the Genus *Salpa*." Among other important researches may be mentioned his studies on the "Lucayan Indians," "Development of Marine Prosobranchiate Gasteropods," "Early Stages in the Development of Fresh Water Pulminates," "The Development of Lingula and the Systematic Position of the Brachiopoda," "The Relationships of Mollusca and Molluscoidea," "The Life History of the Hydromedusæ," "The Stomatopoda of the Challenger Expedition," "Lucifer: A Study in Morphology," "The Embryology and Metamorphosis of the Macroura" (with F. H. Herrick), and a "Monograph of the Genus *Doliolum*."

His studies on the development of mollusks led him to an examination of the life history and habits of the oyster and this was followed by a consideration of the best methods of propagating and cultivating oysters. His work on this subject was embodied in a book called "The Oyster," which has recently appeared in a second edition. Because of its economic importance, Brooks has been more widely known through this work than through any other. He was made chairman of the Maryland Oyster Commission and did much to improve this industry by a scientific treatment of the subject.

He wrote but one text-book, his "Handbook of Invertebrate Zoölogy" (1882) but this was so excellent that it still remains a model, and in some respects has not been excelled, if equalled, by any later book on that subject.

His chief interest was always in the philosophical side of biology and into this he put the larger part of his life work. Even the special researches, some of which have been named above, were permeated by philosophical inquiry, and most of his books and later contributions were devoted to the deeper philosophical meanings of vital phenomena.

As a boy he had read the works of Darwin and had been immensely impressed by them and to the last he yielded to no one in his admiration and reverence for that great master. Probably no other disciple of Darwin was more thoroughly acquainted with his works, and very frequently when criticisms of Darwinism appeared he would point out the fact that the critic did not understand what Darwinism is, or that Darwin had already met and answered the objections raised.

In 1884 he published a book entitled "The Law of Heredity," which in some respects anticipated the theories of Weismann, and which won the highest commendation from Huxley and other leaders of biology. But probably the book by which he will be longest remembered is the series of lectures delivered at Columbia University and published in the Biological Series of that institution under the title "The Foundations of Zoölogy" (1899). In this book he deals with many subjects fundamental not only to zoölogy, but to science and philosophy in general. Among these may be mentioned "Nature and Nurture," "Zoölogy and the Philosophy of Evolution," "Natural Selection and the Antiquity of Life," "Natural Selection and Natural Theology," "Paley and the Argument from Contrivance," "The Mechanism of Nature," "Louis Agassiz and George Berkeley," etc. On the whole his chief points of view may be summarized in his oft-quoted remark of Aristotle that the "essence of a living thing is not what it is made of nor what it does, but why it does it," or as he expresses it elsewhere, "the essence of a living thing is not protoplasm but purpose"; and in the further statements which he draws from Berkeley, that "nature is a language," that "phenomena are appearances," and that "natural laws are not arbitrary nor necessary, but natural, *i. e.*, neither less nor more than one who has the data has every reason to expect."

On March 25, 1898, sixty of his former students united in pre-

senting to him an oil portrait of himself together with a congratulatory address, and at the end of his book on the "Foundations of Zoölogy," he added on this date, the following note:

> "For you who have, at this time, for my encouragement, called yourselves my students, I have written this book which has been my own so long that I should part with it with regret, did I not hope that, as you study the great works to which I have directed you, you may still call me teacher. . . . If you are indeed my students, you are not afraid of hard work, so in this day of light literature, when even learning must be made easy, you must be my readers, and you must do double duty; for I take the liberty of a teacher with his pupils, and ask that, after you have read the book, you will some day read it again; since I hope that what may seem obscure, may, on review, be found consistent and intelligible."

David Starr Jordan review this book in *Science* under the caption "A sage in biology." Whatever one may be inclined to say of his conclusions and theories, it cannot be denied that in an age when biological investigators have been content with discovering phenomena, he has attempted to go back of phenomena to their real meaning and significance and to point out the relationship of these newly discovered phenomena to the great current of philosophy which has flowed down to us from the remote past.

In his philosophical writing he was most deeply influenced by Aristotle, Berkeley and Huxley. Much that he has written still seems to me obscure, although I have read it more than once, but I bear in mind his parting request, and in the meantime profit by that which I do understand and am charmed by the classical and almost poetical diction in which it is written.

His abilities received early and generous recognition. Apart from his university advancement he received many honors. He received the honorary degree of LL.D. from Williams College in 1893, from Hobart College in 1899, and from the University of Pennsylvania at the Franklin Bicentennary in 1906. In 1884, at the age of thirty-six, he was elected a member of the National Academy of Sciences; he was chosen a member of the American Philosophical Society in 1886; of the Academy of Natural Sciences of Philadelphia in 1887; he was also a member of the Boston Society of Natural History, the American Academy of Arts and Sciences, of the Maryland Academy of Arts and Sciences, and of

the American Society of Zoölogists; he was a fellow of the American Association for the Advancement of Science, and also a fellow of the Royal Microscopical Society. For his work on the oyster he received the medal of the Société d'Acclimatation of Paris; for his work on the scientific results of the Challenger Expedition he was given a Challenger Medal; and he received a medal at the St. Louis Exposition of 1904, where he gave an address. He was Lowell Lecturer in Boston in 1901, and he gave one of the principal addresses before the International Zoölogical Congress in 1907.

These honors he highly prized, and perhaps none of them more than his membership in this society. Whenever he was able, he attended the general meetings of the society, and usually presented a paper on some philosophical subject. He served as a counsellor of the society and frequently spoke to me of its purposes and policies. He greatly enjoyed coming into this historic hall, rich in its associations with great men of the past, and on one occasion when I spoke to him of the plan to provide a larger home for the society in a more central part of the city, he said to me, "Do you think you have any right to move the home of the society? It seems to me that you are only trustees of a historic institution, executors of an ancient trust, and that you have no right to remove this monument from its historic site."

In personal character Professor Brooks was simple and child-like, unconventional in manners, dress and speech. With him talking meant expressing ideas, not merely passing the time, and if he had no answer ready when a question was asked him, he usually gave no answer until he was ready. These characteristics made him appear somewhat unique and picturesque, and gave rise to many charming anecdotes about him which his students and friends relate with merriment, but real affection. He was kind and gentle; and neither in his publications nor in his relations with his students did he ever deal in scorn, irony, nor invective. President Remsen said of him that he had been called the most lovable man in the faculty. His interest in his former students was genuine and hearty though he rarely expressed it directly to the person concerned. He was modest and dignified; sincerity itself; loyal to his friends, his university, and his ideals; independent in thought and action, and

not easily moved from a position he had once taken. He was a man of wide culture; he loved the best literature, music and art. When I last saw him at his home we spent the entire evening until after midnight playing, on his automatic piano, great compositions of Beethoven, Mozart, Wagner and other masters of harmony.

In his home life he was most happy and devoted. He married in June, 1878, Amelia Schultz, of Baltimore, by whom he had two children, Chas. E. Brooks, Ph.D., of Elizabeth, N. J., and Menetta W. Brooks, A.B., who, after the death of Mrs. Brooks in 1901, took charge of his home.

Professor Brooks once told me that he proposed to retire from his professorship when he had reached the age of sixty and thereafter devote himself entirely to philosophical and scientific work. He reached the age of sixty last March, but how different was his realization from his plan. His retirement was not to the scholarly leisure for which he longed, but to pain, weakness and mortal sickness. For nine months he struggled against a complication of organic heart trouble and kidney disease and at sunrise on Thursday, November twelfth, he breathed his last.

In his death this society has lost a worthy and devoted member, the world of scholars a man of rare ability and accomplishments, and his friends and associates a noble and lovable companion. Peace to his ashes, honor and reverence to his memory!

EDWIN G. CONKLIN.

PRINCETON UNIVERSITY.